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MASS MUTATION IN OENOTHERA PRATINCOLA[1]

HARLEY HARRIS BARTLETT

(WITH FIFTEEN FIGURES)

Introduction

Of the several small-flowered wild evening primroses thus far examined by the writer for mutability, no other has yielded as valuable data as *Oenothera pratincola*. Certain mutations of this species have been treated in a former article,[2] of which this one is in effect a continuation. To recapitulate very briefly, it may be recalled that *O. pratincola*, a species found wild at Lexington, Kentucky, gives rise in successive generations to a small proportion of mutations, belonging to several distinct types. Of these the most conspicuous in the young condition is mut. *nummularia*, which originates in every generation from seven of the eight independent strains which have been studied. The eighth strain, designated in the former article as Lexington E, shows the phenomenon which the writer has elsewhere designated as mutation *en masse*.[3] Mutant species in *Oenothera*, as typified by *O. Lamarckiana*, give rise to few mutations. The frequency of mutations in

[1] From the Bureau of Plant Industry, U.S. Department of Agriculture, Office of Plant Physiological and Fermentation Investigations. Published by permission of the Secretary of Agriculture.

[2] BARTLETT, H. H., Additional evidence of mutation in *Oenothera*. BOT. GAZ. 59:81–123. 1915.

[3] ———, Mutation *en masse*. Amer. Nat. 49:129–139. 1915.

O. Lamarckiana is about 2 per cent. Some of its mutations are themselves mutable and give 4 per cent or even 6 per cent of secondary mutations.[4] The ordinary strains of *O. pratincola* produce about 2 per cent of mutations,[5] and the true *O. biennis*, of Holland, only about 0.45 per cent.[6] In strains which show mass mutability, however, the number of mutations rises to 50 per cent or even 100 per cent. This is the case with Lexington E.

Lexington E differs from all the other strains of *O. pratincola* (1) in that it gives rise to a characteristic group of four mutations, (2) in that these characteristic mutations occur in such large numbers as to justify the use of the designation mass mutation for the phenomenon, and (3) in that it does not give rise to mut. *nummularia* and certain other mutations which are characteristically produced by the strains which do not show mass mutation.

Turning now to resemblances, we find absolutely no morphological characteristics to indicate even the slightest difference between Lexington E and the other strains of *O. pratincola*. Moreover, Lexington E shows also the ordinary type of mutability, in that it gives rise to small numbers of some of the same mutations which the other strains produce. These mutations are in no wise distinguishable morphologically from the same forms occurring in the other strains, but all the evidence at hand shows that when derived from the strain showing mass mutation the non-characteristic mutations themselves show mass mutability. The mutations characteristic of mass mutability are themselves mutable and throw as secondary mutations other members of the characteristic group.

In view of the extraordinary interest of the phenomenon of mass mutation, it is hoped that the reader will pardon the presentation of this confessedly preliminary report. Many of the genetic relationships between the mutations and the parent species remain to be worked out, and, as will be very obvious, a cytological study of the whole subject is imperative.

[4] DEVRIES, H., Gruppenweise Artbildung. pp. 312–315.

[5] An estimate based upon the results tabulated in BOT. GAZ. **59**:105–109. 1915.

[6] DEVRIES, H., The coefficient of mutability in *Oenothera biennis* L. BOT. GAZ. **59**:169–196. 1915.

The characteristic mutations of the mass mutating strain

The four mutations, which by occurring in such large numbers characterize the hereditary behavior of Lexington E, form a group with a common structural peculiarity which sets them apart from typical *O. pratincola* and from all the other mutations. This peculiarity lies in the narrow, strongly revolute, veiny leaves, of which the midrib is frequently but not always prolonged from a point below the apex as a setiform appendage. This appendage strongly resembles the infra-terminal calyx tips of certain species of *Oenothera*, and suggests the translocation of a character from one organ to another which does not typically display it. The setiform appendage is exceptionally a centimeter long but is entirely absent on some leaves of each individual mutation. It may be said that the four mutations are characterized by the possibility of manifesting the appendage under favorable conditions rather than by its invariable presence. The revoluteness, narrowness, and venoseness of the leaves, however, are characters which are always distinctive.

The four characteristic mutations may be contrasted as follows:

Plants as tall as *O. pratincola* f. *typica*, with a much-branched terminal inflorescence; fruiting freely by self-pollination and producing a normal number of viable seeds ..... mut. *formosa*

Plants semi-dwarf; leaves whitish, broader and thicker than in the last; inflorescence often simple and bearing a few thick-tissued, usually cleistogamous flowers; producing by self-pollination large, apparently normal capsules which contain very few seeds ..... mut. *albicans*

Plants semi-dwarf; leaves green, narrower than in mut. *formosa;* inflorescence densely branched and many-flowered; ovaries almost sterile, producing no capsules by normal self-pollination and only shriveled capsules with few seeds by artificial pollination ..... mut. *revoluta*

More extreme dwarfs, with narrowly linear leaves; inflorescence-bearing branches with broader leaves than the rest of the plant, simple, with thick-tissued, usually cleistogamous flowers which produce large normal fruits but very few viable seeds by natural self-pollination ..... mut. *setacea*

The four mutations do not form a linear series showing successive degrees of reduction. Mut. *formosa* and mut. *revoluta* are very similar and might be interpreted as successive reduction stages. They differ in size and fertility, but have many morphological

characters in common. Before flowering they can be distinguished with certainty only when the environmental conditions are the same for both. Thus, mut. *revoluta* grown in a rich, moist soil is as large as mut. *formosa* grown in a dry, sandy soil. Under such conditions they might be indistinguishable until they flowered, when the latter would produce large capsules, filled with good seeds, and the former would produce few seeds or none in the shriveled ovaries. Grown under identical conditions, however, the two mutations differ at every stage of development. In some features mut. *setacea* also appears to be a reduction derivative in the same series with mut. *formosa* and mut. *revoluta*. In comparison with the latter, however, it shows a partial resumption of fertility. Its large, strong capsules are well filled, although the seeds are for the most part empty. In this characteristic, as also in its simple inflorescences and thick-tissued buds and flowers, it resembles mut. *albicans*. Mut. *setacea* is different from the other three mutations in its strong tendency to produce dimorphic foliage. The rosette leaves and young cauline plants have narrowly linear, grasslike leaves, which are succeeded above and on the inflorescence-bearing lateral branches by leaves much like those of mut. *revoluta*, which nearly always show the setiform terminal appendage. Like the latter mutation, mut. *setacea* responds greatly to environmental changes. In dry sandy soil it flowers and fruits when only 10 cm. high, but in moist loam it becomes 50 cm. high and has quite a different aspect. The comparatively broad-leaved mut. *albicans* is totally unlike the other mutations at every stage of development.

THE F_1, F_2, AND F_3 PROGENIES OF FORMA *typica*

The original wild mother plant designated as Lexington E did not give a progeny in any way peculiar when it was first grown in 1913. A casual inspection of the F_1 seedlings disclosed no mutations. The majority of the plants of this first culture were discarded as very young seedlings and only 30 were brought to maturity. These 30 plants were entirely typical. In 1914 the F_2 of the strain was found to show mass mutation. The remaining seeds of the original collection were therefore sown, in order to detect any mutability which, on account of the use of insufficiently

rigorous experimental methods, might have been overlooked the year before. The results from the new F_1 cultures of 1914 are set forth in table I.

TABLE I

ANALYSIS OF THE F_1 SEEDLING CULTURES OF LEXINGTON E

Culture	Seeds planted	Total plants	Forma *typica*	Mut. *albicans*	Mut. *setacea*	Mut. *latifolia*	Mut. *graminea*
2.....	200*	162	160†	0	1 (no. 35)	1 (no. 36‡)	0
3.....	199*	175	172	1 (no. 34‡)	0	0	2 (nos. 32‡ and 33‡)
4.....	203*	62	62	0	0	0	0
5.....	185*	123	123	0	0	0	0
Total	787	522	517†	1	1	1	2

* Indicates seeds from one capsule.

† 25 plants of f. *typica* from culture 2, grown to maturity, were uniform. The remaining plants of f. *typica* were discarded in the rosette stage.

‡ Indicates that the mutation was grown to maturity.

It is clear from table I that the F_1 did not point to Lexington E as a specially mutant strain. There were only 5 mutations in a progeny of 522 plants. Moreover, 2 of the 4 types obtained, mut. *latifolia* and mut. *graminea*, were common to the other strains of *O. pratincola*.

In 1914, F_2 progenies were grown from 3 plants of *O. pratincola* f. *typica* belonging to strain E, and the progeny of a fourth was grown in 1915. The results are summarized in table II.

The F_2 shows a decidedly greater degree of variability than the F_1. One progeny only, that from Lexington E-5, shows mutations in excess of the number of typical plants; the other three progenies indicate a degree of mutability more comparable with that of certain derivatives of *O. Lamarckiana*, such as *O. scintillans*. The F_1, however, was, if anything, less mutable than *O. Lamarckiana* itself. Successive generations seem to show an increasing degree of mutability. Only one F_3 progeny from f. *typica* has been studied. The parent belonged to the progeny of Lexington E-5, that is, it was selected from the most mutable line. The analysis of the F_3 culture is shown in table III.

The salient fact shown by the data for the F_1, F_2, and F_3 progenies is that the number of mutations varies inversely with the

number of seeds per capsule. The F_1 progeny, with few mutations, came from capsules with about 200 seeds. (Perhaps the capsules

TABLE II

ANALYSIS OF THE F_2 CULTURES OF LEXINGTON E, FROM 4 F_1 F. *typica* PARENTS

Parent	Culture	Seeds planted	Total plants	Forma *typica*†	Mut. *formosa*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations	Percentage of mutations
Lex. E-5 . .	1	156*	131	109	0	0	3	17	2 (no. 208, *angustifolia*)	22	
" . .	2	96*	72	26	0	6	3	36	1 (no. 210, *chimaera*)	46	
" . .	3	106*	75	33	2	6	1	33	0	41	
" . .	4	75*	57	15	1	3	5	33	0	42	
" . .	5	104*	69	10	2	1	4	51	1 (no. 238, *gigas*)	59	
Total . . .	1–5	537	404	194	4	15	15	172	4	210	52
Lex. E-19 . .	1	340*	270	261	0	0	4	5	0	9	
" . .	2	350*	239	224	0	0	4	11	0	15	
" . .	3	219*	150	142	0	0	4	4	0	8	
" . .	4	299*	230	219	0	0	4	7	0	11	
" . .	5	378*	143	108	0	1(no. 67)	7	27	0	35	
Total . . .	1–5	1586	1032	954	0	0	24	54	0	78	7·5
Lex. E-25 . .	1	187*	136	130	0	0	3	3	0	6	
" . .	2	225*	147	142	0	0	1	4	0	5	
" . .	3	186*	145	138	0	0	4	3	0	7	
" . .	4	180*	147	134	0	1	3	9	0	13	
" . .	5	144	72	66	0	0	1	4	1 (no. 34)	6	
Total . . .	1–5	922	647	610	0	1	12	23	1	37	5·7
Lex. E-43 . .	1	410‡	275	238	0	0	1	36	0	37	
" . .	2	424‡	362	328	0	2	4	27	1 (no. 70§)	34	
Total . . .	1 and 2	834	637	566	0	2	5	63	1	71	11

* Seeds from one capsule.

† Plants of f. *typica* were grown to maturity as follows: Lex. E-5, 49 plants from cultures 2, 3, 4, and 5, including all of the *typica* plants shown in figs. 1, 2, 3, 4, and 5; Lex. E-19, 18 plants from cultures 1 and 5; Lex. E-25, 23 plants from culture 5; Lex. E-43, 29 plants from culture 2. The remainder were classified in the seedling stage and discarded. The mutations were all retained and classified at maturity, except that some of the weaker specimens of mut. *setacea* died at various stages of development.

‡ Seeds of two capsules.

§ Lex. E-43-70 was a new mutation combining characters of mut. *nitida* and mut. *angustifolia*, two frequent derivatives of *O. pratincola*.

had dehisced at the apex and lost part of their seeds, as frequently happens. A normal capsule of *O. pratincola* contains 300 seeds,

more or less.) The F_2 progenies of 3 mother plants whose capsules contained an average of about 250 seeds gave about 8 per cent of mutations, the upper limit of ordinary mutability, as far as experience goes. Another F_2 progeny from a mother plant with about 110 seeds to the capsule gave over 50 per cent of mutations. Turning to the very striking F_3 progeny, we find that a mother plant

TABLE III

ANALYSIS OF F_3 CULTURES OF LEXINGTON E, FROM LEX. E-5-229, F. *typica*

Culture	Seeds planted	Total plants	Forma *typica*	Mut. *formosa*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations	Percentage of mutations
1.....	39	30	9	0	1	1	19	0	21	70
2.....	86*	56	6	2	4	4	39	1 (*angustifolia*)	50	89.3
3.....	91*	71	17	0	3	8	43	0	54	76.1
4.....	100*	74	22	0	3	5	42	2 (*gigas?*)	52	70.3
5.....	80*	48	20	3	3	4	18	0	28	58.3
6.....	97*	69	24	0	4	2	39	0	45	65.2
7.....	95*	51	19	0	3	1	28	0	32	62.7
8.....	104*	73	21	0	4	3	44	1(?)	52	71.2
9.....	105*	68	30	0	3	0	35	0	38	55.9
10.....	142*	102	8	0	0	5	89	0	94	92.2
11.....	59*	39	4	0	5	2	28	0	35	89.8
12.....	79*	65	13	0	5	3	43	1 (*gigas?*)	52	80.0
13.....	83*	65	8	1	4	6	46	0	57	87.7
14.....	85*	42	18	1	0	1	22	0	24	57.3
15.....	72*	59	19	2	6	2	30	0	40	67.8
16.....	73*	51	15	1	7	2	26	0	36	70.6
17.....	87*	73	13	0	2	5	53	0	60	82.2
Total..	1477	1036	266	10	57	54	644	5	770	74.3

* Seeds from one capsule; the entire progeny was classified from the young seedlings; 30 plants of f. *typica* and all the mutations except the weaker individuals of mut. *setacea* were retained.

with only 90 seeds to the capsule gave almost 75 per cent of mutations. It would be necessary to have much more complete data to establish any exact relationship between progressive sterility and mutability. Nevertheless, it is beyond question that the decrease in the number of seeds has gone hand in hand with the increase in mutability.

In *Oenothera pratincola*, therefore, the phenomenon which I have termed mutation *en masse* is associated with the failure of a

large number of zygotes to develop, for the number of ovules in all capsules appears to be about the same. Probably the zygotes which fail to develop into embryos represent the weaker individuals of mut. *setacea*, or perhaps some still more reduced mutation which is incapable of development. The problem, however, must be attacked by cytological methods. It is interesting to observe that the F_3, with an average seed germination of 70 per cent, contained 75 per cent of mutations. If all the seeds had germinated, and the additional plants had all been f. *typica*, there would still have been more than 50 per cent of mutations. It seems far more likely, however, that the seeds which did not germinate were either empty or else that they were the weak mut. *setacea*.

A comparable degree of mutability to that of Lexington E is known only in the case of *O. Reynoldsii*, in which mass mutation was first described. In *O. Reynoldsii*, also, the great increase in mutability is associated with an enormously increased degree of sterility. The data in regard to the latter species will soon be published elsewhere.

A number of photographs were made to record the appearance of the mutations at various stages of growth. Figs. 1–5 show a portion of the F_2 progeny from F_1 parent Lexington E-5, recorded in table II. All of the characteristic mutations are shown, as well as several plants which became the parents of subsequent cultures. Fig. 6 shows 6 rosettes of mut. *setacea*, one of which will be found in fig. 3. Fig. 7 shows two mature plants of the same mutation, of which one is shown in fig. 5. Fig. 8 shows 4 rosettes of mut. *revoluta*, 3 of which are likewise shown in figs. 4 and 5. A mature plant is shown in fig. 9. Fig. 10 shows 6 rosettes of mut. *albicans*, 3 of which will be found in figs. 2, 3, and 4. Fig. 11 shows two cauline plants of the same form. The one on the left is just beginning to flower; the one on the right lingered in the rosette condition and would therefore have matured as a stronger plant than its sister. Rosettes of mut. *formosa* are shown in fig. 12. The main stem of the mature plant is shown in fig. 13, and the identical cross mut. *formosa*×f. *typica* in fig. 14. Fig. 15 shows young rosettes of f. *typica* and mut. *gigas*. The *gigas* plant was the particular individual in which E. G. ARZBERGER determined the chromosome

number to be 28. For a figure showing the mature stem of f. *typica* the former article on *O. pratincola* in this journal[2] should be consulted.

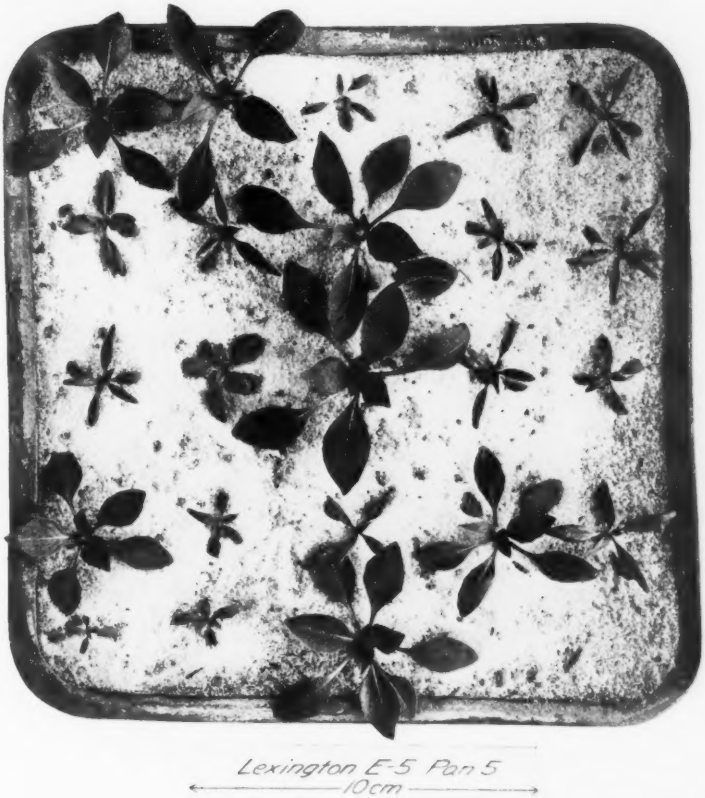

FIG. 1.—Progeny of Lexington E-5, pan 5 (part of culture 2; see table II); the pan contained 23 rosettes which were classified, most of them at maturity, as follows:

Row	1	2	3	4	5
1.....	typica	typica	setacea	setacea	setacea
2.....	albicans	setacea	typica	setacea	setacea
3.....	setacea	albicans (no. 187; see fig. 11)	typica	setacea	setacea
4.....	typica	setacea	setacea	typica	setacea
5.....	setacea	setacea	typica		

Mass mutability of the non-characteristic mutations

It has already been stated that Lexington E gives rise to certain mutations which are common to the other strains of *O. pratincola* from Lexington, and that these non-characteristic mutations, as

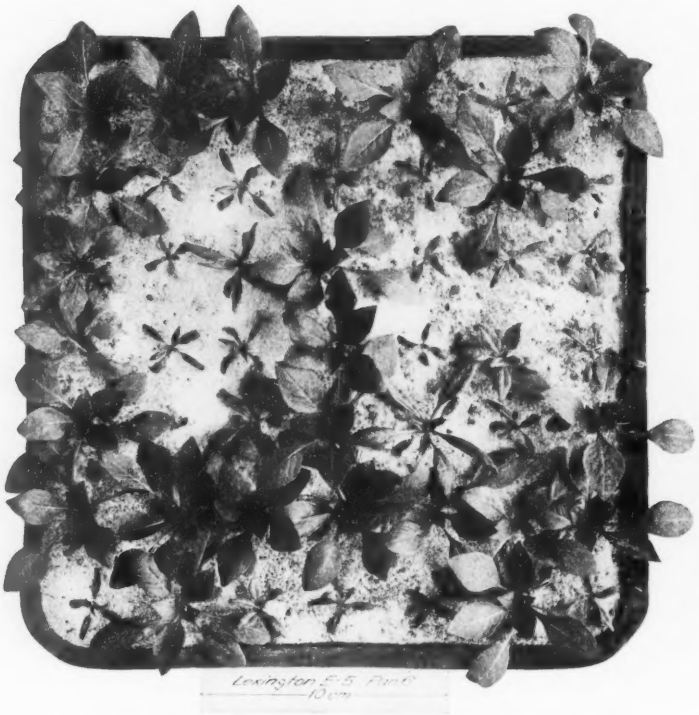

FIG. 2.—Progeny of Lexington E-5, pan 6 (part of culture 3; the remainder is shown in fig. 3; see table II); the pan contains 49 plants, classified as follows:

Row	1	2	3	4	5	6	7
1	typica	typica	typica	setacea	typica	setacea	typica
2	typica	setacea	setacea	setacea	setacea	typica	setacea
3	typica	setacea	setacea	typica	setacea	setacea	albicans (no. 190; see fig. 10)
4	typica	setacea	setacea	typica	setacea	albicans	setacea
5	typica	setacea	setacea	typica	formosa	setacea	typica
6	typica	typica	typica	typica	typica	typica	typica
7	setacea	typica	albicans	setacea	setacea	typica	setacea

they may be called for convenience, exhibit mass mutability superposed upon their ordinary behavior in heredity. In order to present the data in regard to this point it will be necessary to anticipate somewhat the publication of the next article of this series.

Among the mutations of *O. pratincola* which have been obtained both from Lexington E and from the strains showing only ordinary

FIG. 3.—Progeny of Lexington E-5, pan 7 (part of culture 3; the remainder is shown in fig. 2; see table II); the pan contains 26 plants, which were classified at maturity as follows:

Row	1	2	3	4	5	6
1.....	formosa	setacea	albicans (no. 191; see fig. 10)	setacea	setacea	
2.....	typica	albicans	setacea	setacea	typica	
3.....	typica	setacea	setacea	albicans	typica	
4.....	typica	setacea	typica	typica	setacea	
5.....	setacea	setacea	setacea	setacea	setacea	setacea (no. 88; see fig. 6)

mutability, two, mut. *angustifolia* and mut. *latifolia*, have been carried into an F_1 generation from parent plants derived from both sources. A third non-characteristic mutation, mut. *gigas*, has appeared in Lexington E and also, apparently, in the other strains,

FIG. 4.—Progeny of Lexington E-5, pan 8 (part of culture 4; see table II); the pan contains 49 plants, which were classified (most of them at maturity) as follows:

Row	1	2	3	4	5	6	7
1...	typica	setacea	setacea	typica	typica	setacea	setacea
2...	setacea	albicans	typica	setacea	formosa	setacea	setacea
3...	typica	setacea	typica	revoluta (no. 203; see fig. 8)	setacea	typica	revoluta (no. 202; see fig. 8)
4...	setacea	typica	setacea	typica	typica	setacea	setacea
5...	setacea	typica	setacea	typica	setacea	albicans (no. 195; fig. 10)	setacea
6...	setacea	setacea	setacea	setacea	setacea	setacea	setacea
7...	setacea	revoluta	setacea	setacea	setacea	setacea	setacea

but no progenies have yet been grown or chromosome counts made, except in the case of one plant, belonging to the mass mutant strain.

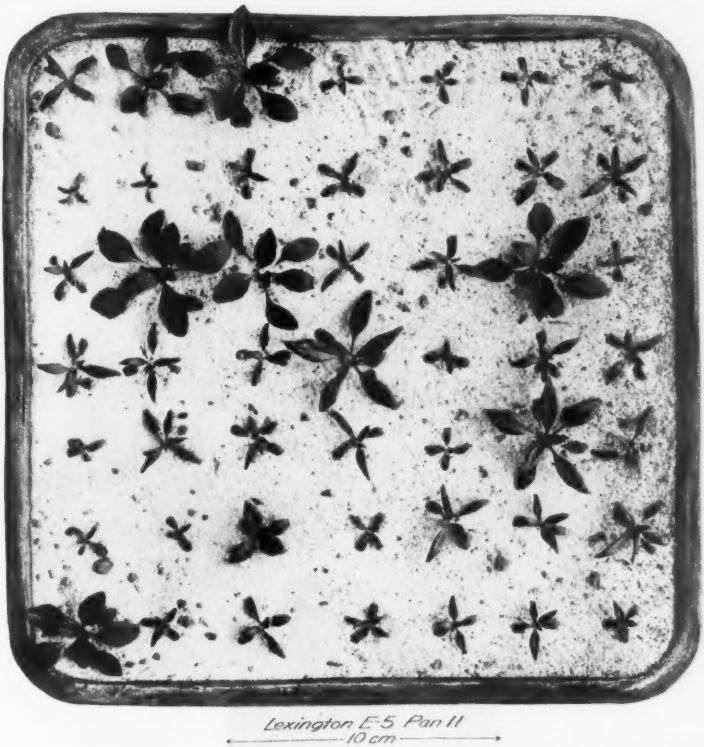

FIG. 5.—Progeny of Lexington E-5, pan 11 (part of culture 5; see table II); the pan contains 49 plants, which were classified (most of them at maturity) as follows:

Row	1	2	3	4	5	6	7
1.....	setacea	gigas (no. 238; see fig. 15)	typica (no. 239; see fig. 15)	setacea	setacea	setacea	setacea
2.....	setacea	setacea	setacea	setacea	setacea	setacea	setacea
3.....	setacea	typica	typica	setacea	setacea	typica	setacea
4.....	setacea	setacea	setacea	formosa (no. 206; fig. 12)	setacea	revoluta	setacea
5.....	setacea	setacea	setacea	setacea (no. 164; see fig. 7)	setacea	formosa (no. 207; see fig. 12)	revoluta (no. 172; see fig. 8)
6.....	setacea	setacea	albicans	setacea	setacea	revoluta	setacea
7.....	typica	setacea	setacea	setacea	setacea	setacea	setacea

(This plant is shown in figs. 5 and 14.) All three mutations are discussed here, but full data and illustrations are reserved for a paper entitled "Certain mutations and hybrids of *Oenothera pratincola*," to appear later in this journal.

Mut. *angustifolia*.—It has been found that mut. *angustifolia* from ordinary strains gives no descendants resembling itself; aside from the usual small proportion of other mutational types, the progeny consisting of f. *typica* only. The variation, although striking and entirely discontinuous, appears to be somatic. In this connection it is interesting to note that a perfect branch of f. *typica* has been observed as a bud sport on mut. *angustifolia*. As would be expected, mut. *angustifolia* crossed reciprocally with f. *typica* gives f. *typica* together with the usual few mutations. The hereditary behavior may be stated:

mut. *angustifolia*×mut. *angustifolia* → f. *typica*
mut. *angustifolia*×f. *typica* → f. *typica*
f. *typica*×mut. *angustifolia* → f. *typica*

The behavior of mut. *angustifolia* from Lexington E is most remarkable. The parent plant was a sister of the *typica* plant whose progeny is analyzed in table III, but the degree of mutability proved to be much more extreme than in the case of the *typica* sister. Only two plants in the progeny, out of a total of 505, were f. *typica;* the other 503 plants, 99.6 per cent of the progeny, were mutations belonging to the group characteristic of Lexington E. The results are summarized in table IV.

The cross mut. *angustifolia*×f. *typica* and the reciprocal gave respectively 100 per cent and 91.5 per cent of mutations. By comparison with table III it will be seen that each of the reciprocal crosses tends to show the same degree of mutability as the female parent. To be sure, there would seem to be a considerable discrepancy between 74.3 per cent, representing the mutability of f. *typica*, and 91.5 per cent, representing the mutability of f. *typica* ×mut. *angustifolia*. No significance can be urged for this discrepancy, however, when we consider that one of the cultures from a single capsule of f. *typica* contained 92.2 per cent of mutations among 102 plants, as compared with 91.5 per cent of mutations

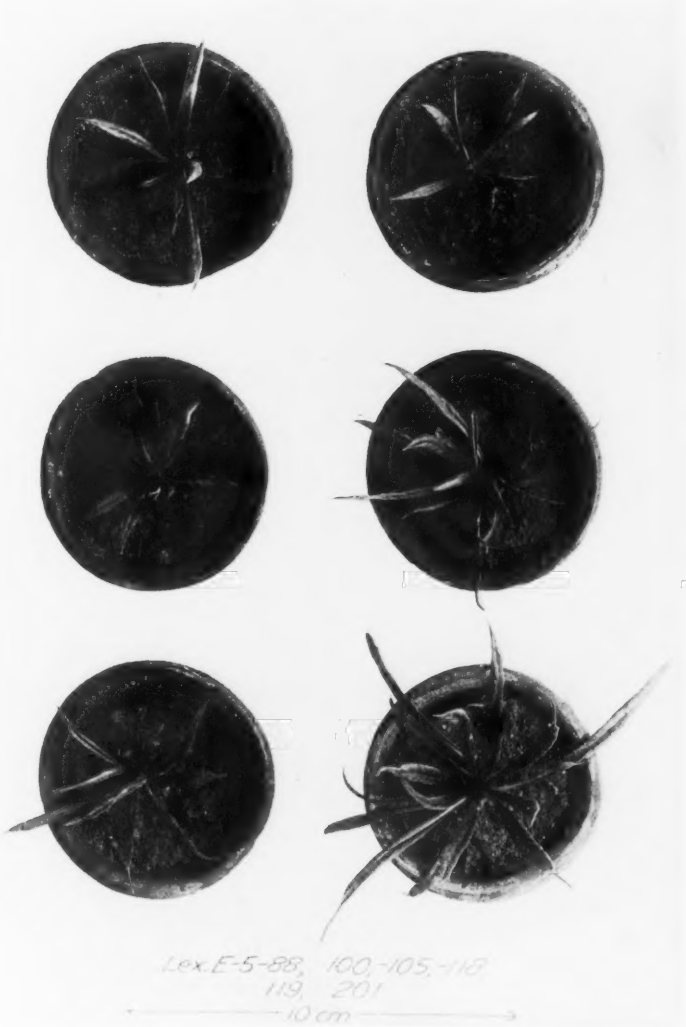

FIG. 6.—Mut. *setacea:* 6 rosettes of the F_2 progeny of f. *typica*, from F_1 parent Lexington E-5; the plant in the upper left-hand corner, Lexington E-5-88, is shown also in fig. 3.

among 118 plants of the cross. As a matter of fact, the significance of ratios in *Oenothera* can be maintained only with great caution, in view of the enormous elimination of gametes during maturation and the subsequent failure of large classes of zygotes to develop. Nevertheless, the absence or almost complete absence of a strong zygote such as f. *typica* in the progenies of mut. *angustifolia* and mut. *angustifolia*×f. *typica* is strong evidence for the view that the composition of the progeny among the mass mutating strains is conditioned by the female gametes. The failure of a

TABLE IV

ANALYSIS OF F_1 CULTURES OF MUT. *angustifolia*, LEXINGTON E-5-208, SELF-POLLINATED AND RECIPROCALLY CROSSED WITH F. *typica*, LEXINGTON E-5-229 (THE PLANT WHOSE PROGENY IS ANALYZED IN TABLE III)

The mutation was a sister plant of the *typica* plant with which it was crossed; for position in pedigree see table II, culture 1 from Lexington E-5

Parent	Seeds planted	Total plants	Forma *typica*	Mut. *formosa*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations	Percentage of mutations
Mut. *angustifolia*..	651*	505	2	4	2	21	475	1 (no. 1)	503	99.6
Mut. *angustifolia* ×f. *typica*.....	199†	173	0	0	0	4	168	1 (no. 1)	173	100
F. *typica*×mut. *angustifolia*.....	182‡	118	10	0	1	4	99	4	108	91.5

* The 651 seeds were from 11 capsules, containing respectively 51, 75, 53, 62, 44, 59, 82, 101, 46, 33, and 45 seeds.

† The 199 seeds were from 3 capsules, containing respectively 73, 47, and 79 seeds.

‡ The 182 seeds were from 2 capsules, containing respectively 79 and 103 seeds.

class of strong zygotes to appear has much greater evidential value than any fluctuation in the proportion of weak zygotes. From other sources the evidence is unusually strong that the female and male gametes of *O. pratincola* are not equivalent, and that many characters are not carried by the male gametes.

In conclusion: mut. *angustifolia* ordinarily gives a progeny containing nearly 100 per cent of f. *typica;* in a strain exhibiting mass mutation many of the *typica* plants are replaced by mutations of the characteristic group. Presumably other individuals of mut. *angustifolia* could be found which would be less mutable than the one tested, just as different individuals of f. *typica* show widely

varying degrees of mutability. The progenies of crosses indicate that mass mutability is conditioned by the female gametes.

Mut. *latifolia*.—In contrast with mut. *angustifolia*, mut. *latifolia* reproduces itself in part of its progeny. Its descendants include roughly 50 per cent f. *typica* and 50 per cent mut. *latifolia*, the proportion varying within rather wide limits. Moreover, mut. *latifolia* gives progenies of the same type whether self-pollinated or

FIG. 7.—Mut. *setacea:* 2 mature plants from the F_2 progeny of f. *typica*, from F_1 parent Lexington E-5; the right-hand plant, Lexington E-5-164, is shown also in fig. 5; note particularly the dimorphic foliage.

cross-pollinated with f. *typica*. The reciprocal cross, with f. *typica* as the pistillate parent, consists only of f. *typica*, aside from the usual low proportion of mutations, among which mut. *latifolia* may or may not happen to occur. These relations are as follows:

mut. *latifolia*×mut. *latifolia* → f. *typica*+mut. *latifolia*
mut. *latifolia*×f. *typica* → f. *typica*+mut. *latifolia*
f. *typica*×mut. *latifolia* → f. *typica*

The type of heredity here exemplified is shown by several mutations from *O. Lamarckiana*. *O. lata* DeVries provides the classic case. The heredity of *O. scintillans* DeVries and *O. oblonga*

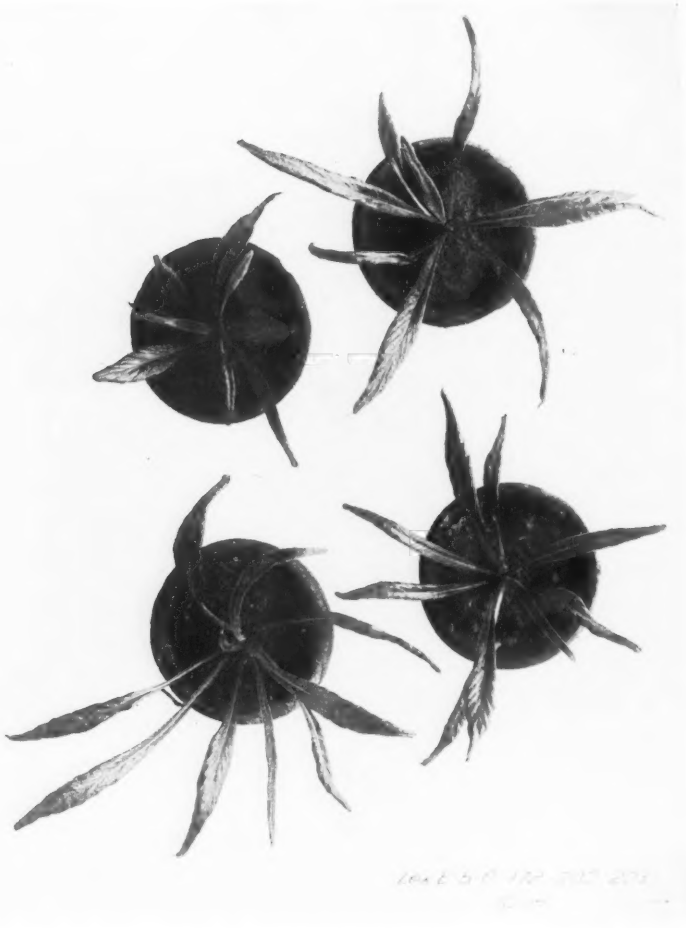

FIG. 8.—Mut. *revoluta:* 4 rosettes of the F_2 progeny of f. *typica*, from F_1 parent Lexington E-5; the upper right-hand plant, Lexington E-5-172, will be found in fig. 5; the two lower plants, nos. E-5-202 and 203, will be found in fig. 4.

DeVries is in essentials the same.[7] Another case is provided by *O. stenomeres* mut. *lasiopetala*.[8] HERIBERT-NILSSON[9] has recently described several new mutations from *O. Lamarckiana* ("heterogame Kombinanten" *dependens*, *undulata*, *stricta*, etc.) which probably show the typical *lata* type of inheritance, although he erroneously concludes that the repeated segregation of *O. Lamarckiana* from these mutations in each generation is due to the existence of two types of functioning gametes on the male rather than on the female side.

It must not be inferred from the similarity of the names that mut. *latifolia* is a parallel variation to *O. lata* DeVries. Such is not the case. Its characters are quite different. Both mut. *latifolia* and mut. *angustifolia* will be described and illustrated in a future article.

As in the case of mut. *angustifolia*, the progeny of mut. *latifolia* from the mass mutating strain contained the expected types, f. *typica* and mut. *latifolia*, together with the characteristic mutations. The latter did not show differences among themselves which would enable one to classify them as modified *typica* or modified *latifolia*, as the case might be. The mother plant belonged to the F_1 generation from Lexington E, and showed about the same degree of mutability as the *typica* sister plant, Lexington E-5 (see table II). The data for mut. *latifolia* are summarized in table V.

Mut. *gigas*.—E. G. ARZBERGER's discovery that this mutation has 28 chromosomes has already been announced.[10] The count has been made only in one plant, Lexington E-5-238 (figs. 5 and 14), belonging to the mass mutant strain. An apparently identical mutation in one of the other strains has appeared this summer (1915), but its heredity is unknown. Mut. *gigas* is treated, therefore, as a non-characteristic mutation. Only 196 seeds were

[7] For the latest treatment of these mutations see DEVRIES, Gruppenweise Artbildung. pp. 244–267.

[8] BARTLETT, H. H., The mutations of *Oenothera stenomeres*. Amer. Jour. Bot. **2**: 100–109. 1915.

[9] HERIBERT-NILSSON, N., Die Spaltungserscheinungen der *Oenothera Lamarckiana*. Lunds Universitets Arsskrift. N.F. Avd. 2. **12**: no. 1. pp. 132. 1915.

[10] BARTLETT, H. H., The experimental study of genetic relationships. Amer. Jour. Bot. **2**:132–155. 1915 (see p. 143).

obtained from 15 capsules of the primary mutation, Lexington E-5-238. The progeny consisted of 25 plants, only 16 of which survived transplanting from the seed pan. None of the progeny resembled the parent. All were extreme dwarfs which resembled, but were not identical with, mut. *revoluta* and mut. *setacea*. They differed mainly in the thicker leaves, which in 4 plants were narrow but not markedly revolute. Although a very nondescript lot, differing much among themselves, 5 most resembled mut. *revoluta*, and 7 mut. *setacea*. The result of this culture might almost have been predicted. The mass mutability was inherited by mut. *gigas* from f. *typica*. In view of the dependence of the *gigas* characters upon

TABLE V

ANALYSIS OF AN F_1 CULTURE FROM SELF-POLLINATED MUT. *latifolia*, LEXINGTON E-36

The parent plant belonged to the F_1 from Lexington E, f. *typica;* see table I, culture 2, for position in pedigree

Parent	Seeds planted	Total plants	Forma *typica*	Mut. *latifolia*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations‡	Percentage of mutations‡
Lex. E-36, mut. *latifolia*.....	375*	182	95	48	5	2	29	3†	87	47.8

* Seeds from 7 capsules, containing respectively 54, 72, 49, 30, 38, 70, and 62 seeds.

† Nos. 32 and 43, a new mutation; no. 51 mut. *gigas (?)*, morphologically identical with Lexington E-5-238 which had 28 chromosomes; see table II, culture 5 from Lexington E-5, for position of latter plant in pedigree.

‡ Excluding, of course, mut. *latifolia*.

the double complement of chromosomes, which would in general be handed on to any secondary mutations, it follows that the mutations occurring *en masse* would not be identical with those from f. *typica*. Furthermore, chance irregularities in chromosome distribution might increase the polymorphism of the progeny. In such a highly modified germ plasm irregularities would be expected.

The cross mut. *gigas*×f. *typica* yielded 160 seeds in a single capsule, of which 10 germinated. The plants were all extreme dwarfs, of the most nondescript nature, hardly any two alike. All had thick leaves, some plane, others revolute. No mutation of

f. *typica* could be identified among them. The reciprocal cross yielded no seeds.

Inheritance and mutability of the characteristic mutations

Of the group of characteristic mutations, including mut. *formosa*, mut. *albicans*, mut. *revoluta*, and mut. *setacea*, only the first is both normally fertile and vigorous. The second is vigorous, but produces few good seeds. The third is almost sterile, and the fourth is not only difficult to cultivate, but like mut. *albicans* gives very few good seeds. All of the forms were self-pollinated and reciprocally crossed with f. *typica* in 1914, but, except in the case of mut. *formosa*, the resulting F_1 cultures were very fragmentary or entire failures. The other three forms bloomed in September, when only a few weak, belated flowers of f. *typica* were available for the crosses. The results of the cultures are summarized in table VI.

FIG. 9.—Mut. *revoluta:* a mature plant, Lexington E-19-21 (for position in pedigree see table II).

Mut. *formosa*.—The entirely satisfactory cultures of this form show that it is constant in the sense that it gives no reversions to f. *typica* in its progeny. Moreover, there is no

TABLE VI

ANALYSIS OF F_1 CULTURES IN THE GROUP OF MUTATIONS CHARACTERISTIC OF MASS MUTABILITY

Parentage culture	Seeds planted	Total plants	Forma *typica*	Mut. *formosa*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations
Mut. *formosa* Lex. E-5-199 × f. *typica* Lex. E-5-217 — 1	244*	196	0	171	0	1	24	0	25
2	269*	163	0	137	0	0	26	0	26
3	201*	177	0	149	0	2	26	0	28
4	216*	174	0	130	1	0	43	0	44
5	217*	193	0	150	0	1	42	0	43
6	224*	179	0	146	0	0	33	0	33
Total 1–6	1371	1082	0	883	1	4	194	0	199
Mut. *formosa* Lex. E-5-199 × f. *typica* Lex. E-5-217	365†	309	0	218	0	0	91	0	91
Mut. *formosa* Lex. E-5-206	177‡	146	0	130	2	0	14	0	16
Mut. *formosa* Lex. E-5-206 × f. *typica* Lex. E-5-229	233§	177	0	151	0	3	23	0	26
F. *typica* Lex. E-5-229 × mut. *formosa* Lex. E-5-206	246‖	133	7	0	1	0	121	4	126
Mut. *albicans* Lex. E-19-67 (seeds of 4 capsules)	386	265	0	0	36	3	226	0	229
Mut. *albicans* Lex. E-5-182 (seeds of 4 capsules)	173	69	0	0	7	3	59	0	62
F. *typica* Lex. E-5-229 × mut. *albicans* Lex. E-5-182	22*	14	1	0	0	1	12	0	13
Mut. *revoluta* Lex. E-5-190 (seeds of 14 capsules)	85	23	0	0	1	17	5	0	6
Mut. *setacea* Lex. E-5-17 (seeds of 4 capsules)	625	140	0	0	0	0	140	0	0
Mut. *setacea* Lex. E-5-20 (seeds of 16 capsules)	1997	8	0	0	0	0	8	0	0
Mut. *setacea* Lex. E-5-66	114*	31	0	0	0	0	31	0	0
Mut. *setacea* Lex. E-5-135 (seeds of 3 capsules)	463	14	0	0	0	0	14	0	0

* Seeds from one capsule.

† Seeds from 2 capsules; 215+150.

‡ Seeds from 2 capsules; 48+129.

§ Seeds from 2 capsules; 64+169.

‖ Seeds from 2 capsules; 115+131.

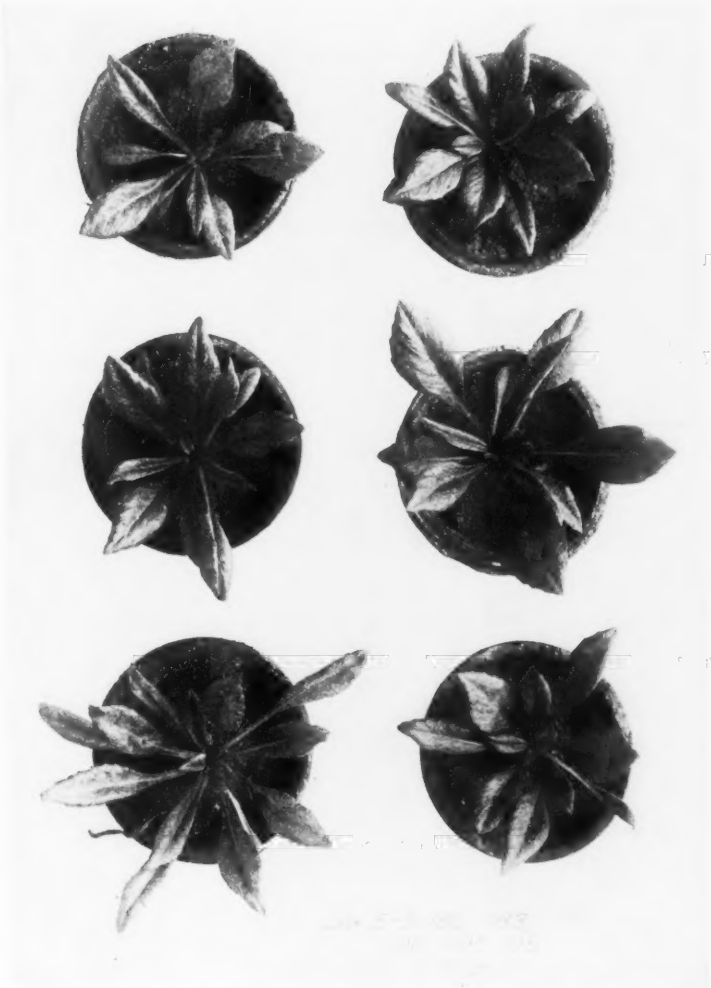

FIG. 10.—Mut. *albicans:* 6 rosettes of the F_2 progeny of f. *typica*, from F_1 parent plant Lexington E-5; the right-hand plant in the middle row, Lexington E-5-190, will be found in fig. 2; the two plants in the lower row, E-5-191 (left) and 195 (right), will be found respectively in figs. 3 and 4.

difference between the progenies resulting from self-pollination and those resulting from pollination with f. *typica*. In other words, mut. *formosa* is dominant over f. *typica* if it enters the cross as a female gamete, but is not even dominant over the weak mut. *setacea* when the *formosa* gamete is male. The scheme of heredity is:

mut. *formosa*×mut. *formosa* → mut. *formosa*
mut. *formosa*×f. *typica* → mut. *formosa*
f. *typica*×mut. *formosa* → f. *typica*

It would have been instructive to cross mut. *formosa* reciprocally with f. *typica* from a non-mass mutant strain. (Such crosses have been made this year and will be grown next year.) From the data at hand, concerning only crosses within the mass mutant strain, it appears clear that the external features of all the characteristic mutations are determined by the female gametes. The female and male gametes are not equivalent. Thus, the progeny obtained from f. *typica*, Lex. E-5-229, by pollination with mut. *formosa* is not significantly different from the progeny obtained by self-pollination (cf. tables III and VI). The characteristic mutations occur with their usual frequency regardless of which pollen is used. We know that this particular individual of f. *typica* gave about 1 per cent mut. *formosa* when grown in large cultures from self-pollinated seeds. That pollination with pollen of mut. *formosa* does not increase the proportion of this mutation in the progeny is strikingly shown by the absence of even a single individual among the 133 plants of the cross. In a culture of this size from self-pollinated seed the chances are about even that an individual of mut. *formosa*, with a frequency of 1 per cent, would or would not turn up. If the use of *formosa* pollen had appreciably increased the frequency of this form in the progeny, a culture of 133 plants might have been expected to show it. The results can be interpreted in only one way, that is, the female gamete carries all the factors which determine the visible characters of the several forms, not only of the 4 mutations, but of f. *typica* as well.

Both parent plants of mut. *formosa* showed a high degree of mutability themselves, and gave rise to the other 3 characteristic

mutations. As in the case of progenies from f. *typica*, mut. *angustifolia*, and mut. *latifolia*, the predominating form among the mutations was mut. *setacea*.

FIG. 11.—Mut. *albicans:* 2 cauline plants, Lexington E-5-196 (left) and 187 (right), from the F_2 progeny of f. *typica;* no. 187 is shown also in fig. 1.

Mut. *albicans*.—This mutation reproduces itself in only a small proportion of its progeny, but can be said to come true in the sense

that it gives no reversions to f. *typica*. All of the aberrant plants in the cultures, both from self-pollination and from pollination with f. *typica*, are mutations belonging to the characteristic group. As in the case of mut. *formosa*, most of the secondary mutations were mut. *setacea*.

The small culture of f. *typica*×mut. *albicans* emphasizes the fact that the composition of the culture is conditioned by the female gamete. As in the case of the analogous cross f. *typica*×mut. *formosa*, the progeny is just what we should expect from self-pollination of the *typica* parent.

FIG. 12.—Mut. *formosa:* 2 rosettes, Lexington E-5-206 and 207, from the F_2 progeny of f. *typica;* both are shown in fig. 5.

Mut. *revoluta*.—Only one small progeny was obtained from this nearly sterile mutation. It showed that the form reproduces itself except for throwing other mutations of the characteristic group. None of the crosses made with mut. *revoluta* were successful, but there can be little doubt, from collateral evidence, that mut. *revoluta*, as well as mut. *albicans*, follows the same type of inheritance as mut. *formosa*.

Mut. *setacea*.—So far as can be determined, this form comes entirely true from seed, and represents the most extreme modification which can take place in the direction followed by the group of characteristic mutations. Although the crosses with f. *typica* have so far not been successful, it is probable that this extreme reduction phase would also be dominant when introduced into the cross as the female gamete.

The numerical data for mut. *setacea* in all cultures have had to be based largely on the determination of very young plants, for many weak plants do not succeed in forming new roots after being transplanted. There is no difficulty in growing to maturity practically every individual of mut. *formosa* that germinates, and most of those of mut. *albicans* and mut. *revoluta*. It is the rule rather than the exception, however, to lose three-fourths or more of the *setacea* plants. They show some variation among themselves which may possibly indicate that mut. *setacea* is itself mutable and that more than one type is covered by this name. If so, only one type survives in the part of the cultures which reaches maturity.

FIG. 13.—Mut. *formosa* (Lexington E-5-206-51): the setiform leaf appendages show very clearly; the position of the plant in the pedigree may be determined from table VI.

The phenomenon of mass mutation

From the results of the crosses between f. *typica* and muts. *formosa* and *albicans*, as well as from the insignificant variation in the composition of cultures showing mass mutation regardless of the source of the pollen, it appears clear that the factors responsible for the mutational characters are carried in the

female gametes. So far, there is no evidence that the pollen of any of the characteristic mutations differs from that of f. *typica*. It follows that mass mutation in *O. pratincola* must be due to the wholesale modification of female gametes. The relations have not been worked out in the case of *O. Reynoldsii*, which also shows mass mutability.

FIG. 14.—Mut. *formosa*×f. *typica* (Lexington E-5-206×E-5-229, one of the F_1 progeny): this cross is identical with mut. *formosa* itself (cf. fig. 13); the constitution of the F_1 progeny is given in table VI; the progenies resulting from self-pollination of the parent plants are recorded in tables III and VI.

There can be no doubt that mass mutation is not Mendelian segregation, although the two phenomena have points of resemblance. HERIBERT-NILSSON'S hypothesis to account for the mutability of *O. Lamarckiana* depends upon the segregation of plural factors for the same character, and involves such complications as the elimination of all zygotes which are homozygous with regard to the presence of any of the numerous plural factors. Needless to say, he has also relied upon the doctrine of the equivalence of male and female gametes. His last paper bears evidence that his faith in the equivalence of gametes is beginning to waver, although he has formerly trusted so

implicitly that he has made crosses only one way. If he had studied the reciprocals of his crosses it is safe to assume that he would never have advanced his Mendelian explanation of mutability. As far as his results extend, his derivatives of *O. Lamarckiana* fall, for the most part, into two classes, which conform in hereditary behavior to the two main classes of mutations which have been obtained from *O. pratincola*.

FIG. 15.—Mut. *gigas* (above) and f. *typica* (below): rosettes from the F_2 progeny of f. *typica;* the rosette of mut. *gigas*, Lexington E-5-238, had a darker color and more conspicuous pubescence than the sister plant of f. *typica*, but the difference does not appear in the photograph; both plants are shown in fig. 5.

Class I.—The mutation breeds true, in the sense that it gives no reversions to the parent form. The reciprocal crosses with the parent species are matroclinic. The progeny conforms to the type which supplies the female gamete.

Class II.—The mutation gives a progeny consisting of the parental and mutational types in greatly varying proportions. The progenies from reciprocal crosses are mixed if the mutation supplies the female gametes, but consist of the parental type only if the mutation supplies the male gamete.

Several mutations of each class have been studied by the writer in more or less detail, and the results will soon be published. As already announced,[11] the interesting mut. *nummularia* belongs to class I, as do also all of the mutations characteristic of Lexington E. Mut. *latifolia* is a typical member of class II. There are mutations, of course, which show neither type of behavior, but they need not be involved in the present discussion.

HERIBERT-NILSSON's hypothesis demands the recessiveness of mutations of class I, regardless of which way they are crossed with the parent. This condition is not fulfilled. It demands that the female gametes of the mutations of class II should be of one kind, and the pollen of two kinds. Neither is this condition fulfilled. His hypothesis makes no provision for the appearance of mutations in excess of one-third of the progeny. In this respect it is quite inadequate. On Mendelian grounds it is as difficult to account for too many mutations as for too few. His assumption is that after a homozygous and recessive condition has been attained in *O. Lamarckiana*, except for one of the plural factors which produce the *Lamarckiana* phaenotype, monohybrid splitting will take place. The one-fourth of dominant homozygotes will be eliminated, and therefore the progeny will consist of heterozygotes and recessives (mutations) in a 2:1 ratio. He has not attempted to explain how more than one-third of a progeny can consist of mutations, although he states in a vague and general way that the discovery of highly mutable strains is an argument in favor of his thesis. Nothing, he says, has made the mutation phenomena appear so exceptional as the low frequency of mutations. In his opinion, the high mutability of *O. Reynoldsii* has rendered the mutation fiction an absurdity.

Further comment on this opinion is rendered unnecessary by the serious discrepancies between HERIBERT-NILSSON's hypothesis and the facts. It can do no harm to point out, however, that even if mutations appeared through the operation of Mendelian segregation, as no one denies may sometimes be the case, it is still necessary to account for the origin of heterozygosis in the parent strain. The writer believes that mutations may often appear as a result of segregation, but that the antecedent heterozygosis has its origin in a mutative change. To attempt to account for the hetero-

[11] Amer. Jour. Bot. 2:146. 1915.

zygosis by hybridization leads to such absurdities as the denial that new forms have ever originated except by hybridization and recombination.

It is perhaps unwise to hazard even a guess at the nature of the modification of the female gametes which results in mass mutation. At one time the writer was inclined to believe that the modification had involved the cytoplasm rather than the nucleus, and that cytoplasmic inheritance might account for the matroclinic crosses. However, there are now adequate data at hand to show that similar matroclinic crosses in other cases cannot be explained by cytoplasmic inheritance. The reason for discarding this hypothesis will be explained in a future paper, since it involves data which cannot be touched upon here.

Mendelian expectations require that the largest class in a progeny showing mutation shall consist of the parent phaenotype. No explanation of the high mutability of mass mutating strains can be accepted which requires the elimination of zygotes of this phaenotype, which according to all other experience are strong and viable. If a deficiency in any class of zygotes were to be expected in a mass mutant strain, it would be the class of weakest mutations; in the case of *O. pratincola*, for example, it would be mut. *setacea*. Yet this mutation is the very one which occurs in the largest numbers.

Mass mutation is neither more nor less easily explained than ordinary mutation. It seems to be due to sudden mutative transformations of certain female gametes, and to be apparent in the zygotes without the necessity of subsequent segregation because of the fact that the factors involved have no counterparts in the male gametes. There is no real distinction between mass mutation and ordinary mutation except that in the former type large numbers of gametes may be simultaneously affected, whereas in the latter only a few are affected.

Summary and conclusions

1. Mass mutation consists in the production of unexpectedly large numbers of mutations, in some cases amounting to 100 per cent of the progeny.

2. The phenomenon is known in two species of *Oenothera: O. Reynoldsii*, in which it was first described, and *O. pratincola*, the subject of this paper.

3. It cannot be explained by HERIBERT-NILSSON'S Mendelian hypothesis.

4. The mutations of the mass mutant strain of *O. pratincola* are: (A) common to other strains of the species; the non-characteristic mutations are not produced in unexpected numbers and show mass mutability superposed upon their ordinary behavior in heredity; (B) characteristic of the mass mutant strain.

5. The characteristic mutations are constant in that they do not throw the type form of the species, but, except in the case of the most reduced member of the group, are themselves highly mutable.

6. As far as tested, the characteristic mutations adhere to the following scheme of inheritance:

mutation × mutation → mutation
mutation × parent → mutation
parent × mutation → parent

7. They belong to a group with certain structural characters in common, but do not seem to form a linear reduction series.

8. They seem to result from the mutative modification in the female gametes of factors which have no counterparts in the male gametes.

9. Mass mutation is associated with a high degree of sterility, which manifests itself in the production of a greatly reduced number of seeds or in the production of many empty seeds.

UNIVERSITY OF MICHIGAN

FERTILIZATION IN ABIES BALSAMEA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 210

A. H. HUTCHINSON

(WITH PLATES XVI–XX AND ONE FIGURE)

A general account of fertilization and the related phenomena in this species has been given by MIYAKI (19). A number of supernumerary nuclei were noted in the micropylar end of the egg at the time of fertilization. These were generally regarded as derived from the male gametophyte, while in some cases another nucleus, that of the ventral canal cell, was added to the number. Repetition has been avoided, inasmuch as the present account is restricted to special problems, while the general account has received little attention.

The problems suggested by the regular occurrence of four nuclei in the egg cytoplasm, near the micropylar end, at the time of the 4-nucleate proembryo, and by the unusual grouping of chromosomes during the division which follows the conjugation of the egg and sperm nuclei, have led to this investigation. Special attention, therefore, will be given to the fertilization of the nucleus of the ventral canal cell and to the cytological features connected with the fertilization of the egg.

The material was collected in Ontario, Canada. I am greatly indebted to Professor W. R. SMITH for collections made at Lake Joseph. On June 25 and 26 I obtained ovules showing fertilization at N. lat. 44°, W. long. 79°12′, and on July 2 and 3 ovules showing similar stages at N. lat. 45°30′, W. long. 78°32′. The altitude in the first case was 900 feet; in the second 1800 feet.

In a former paper on the male gametophyte of *Abies* (10), the excessive number of prothallial cells has been recorded. One of these polar cells, during mitosis, is shown in fig. 1. Fig. 5, which was drawn from a pollen grain lodged in the micropyle, shows the division of the body cell nucleus, to form two male nuclei, taking place before the tube breaks through the spore coat. At this time the cytoplasm surrounding the tube nucleus is extremely vacuolate,

that of the body cell very dense. The tube nucleus begins to disintegrate before the pollen tube emerges from the exine; usually during the pollen tube stage it appears only as an irregular aggregation; seldom, if ever, does it enter the egg.

A number of gametophytes have been found similar to that shown in fig. 2. The first division has cut off a polar ("prothallial") cell which later has disintegrated; the second division has given rise to two equivalent cells; which of the two might have been regarded as prothallial, under other circumstances, is impossible to determine. Evidently there are two antheridia. The conclusions based on a study of *Picea* (**9**), namely, that under favorable conditions any of the cells resulting from the three primary divisions of the male gametophyte may be antheridial, are supported by the facts as found in *Abies*.

The period of time between pollination and fertilization is from four to five weeks. During the greater part of this time the pollen grains lie dormant on the nucellus, or lodged in the micropyle. The course of the pollen tube is direct, and the motion rapid. Although the rate is difficult to determine, it is believed that the passage time of the pollen tube does not exceed two days, and probably may be measured in hours.

Fertilization of the ventral canal cell

The division of the central cell to form the egg and the ventral canal cell is similar to that in *Pinus* (figs. 7, 8, 9; compare, 3, 5, 6, 19); the nuclei formed are similar in size and form. The egg nucleus at once begins to move toward the center of the egg cytoplasm (fig. 7). What the attractive force may be is unknown, but the nucleus of the ventral canal cell responds to the same force and moves in the same direction. This nucleus breaks through the cell wall and enters the cytoplasm of the egg (figs. 11, 12); here it increases in size until it reaches a length, in some cases of 80 μ, which is approximately one-half of the greatest length attained by the egg nucleus. The structure of the ventral nucleus is very similar to that of the egg, which will be described later. The latter is surrounded by a dense granular layer which is not present in the case of the former.

The fertilization of the nucleus of the ventral canal cell has been seen in several instances. One of the male nuclei fuses with the ventral nucleus (figs. 15, 17, 21); the stalk nucleus also may be in close proximity (figs. 17, 18). Sometimes two tubes enter the archegonium, in which case male nuclei from different gametophytes may fuse with the ventral nucleus and egg nucleus respectively (fig. 21). The chromatin of the fusion nucleus condenses near its center (fig. 18), and the first division takes place. Two successive divisions (figs. 16, 23, 24, 26) result in four nuclei, which as might be expected, are generally arranged in pairs (figs. 22, 25). The nuclei of this ventral proembryo range in diameter from 40 to 50 μ; those of the proembryo proper from 60 to 65 μ; otherwise the similarity is very marked (figs. 32, 53, 54).

Nuclear changes

The changes in size of the nuclei located in the egg cytoplasm are the most readily measured of all the modifications; moreover, the increase or decrease in volume will serve to indicate the extent of the qualitative changes which occur. Immediately after the division of the central cell the egg nucleus measures about 30 μ in diameter (fig. 7). At the time of fusion its length approximates 100 μ (fig. 19); during the approximation of the chromatin groups 160 μ is the maximum measurement (fig. 27), and during anaphase of the first division the diameter is again reduced to 50 or 60 μ (fig. 46). The changes in size of the daughter nuclei are less marked; the diameter varies from 20 μ at telophase (fig. 52) to 65 μ in the resting stage It is not surprising that the egg nucleus should vary greatly in structure while increasing to 60 times its original volume, and again decreasing to one-tenth its attained volume.

During the early stages of the first division, and even before the chromatin groups have united, four differentiations of the "nuclear" material are evident. The chromatin group or groups occupy less than one-tenth of the space within the nuclear membrane (figs. 27, 28, 42). The spindle fibers are intranuclear in origin (fig. 28). Large, vacuolate, irregular, deeply staining masses are distributed throughout the whole area. The greater part of the nuclear cavity is pervaded by slender filaments, which

include small granules. An attempt has been made to trace these structures from their origin to their fate, in order that something regarding their nature and function might be determined. This complexity of structure is in contrast with the prophase of an ordinary mitosis, where only chromosomes, at most chromosomes and the nucleolus, are inclosed by the nuclear membrane.

The dark vacuolate masses are most conspicuous just after fusion (fig. 27). In the early stages small refractive globules are scattered throughout the granular egg nucleus; later, these become inclosed in a gelatinous network (fig. 19), and next appear as previously described. During the first mitosis they accumulate into several globular, vacuolate bodies (fig. 34). The latter decrease in volume or become distributed throughout the nucleus during metaphase (fig. 46). At anaphase the irregular masses once more become conspicuous (fig. 51). When the daughter nuclei are formed, these bodies are not included, and soon disappear. The fact that they are extruded would seem to indicate that they are not fundamental nuclear material. The fact that they are stored up during the growth of the nucleus and decrease in amount during mitosis would suggest that they are simply stored food bodies.

Two successive groups of intranuclear fibers become differentiated during the processes of fusion, and the first division after conjugation. The first is concerned with the approximation of chromosomes to be described later; the second with the first mitosis. While the two chromatin groups, from the egg and from the male nucleus, are still distinct, fibers which penetrate and surround these groups are organized (fig. 28). A union of the two groups of fibers results in the formation of a single spindle made up of large complex strands (figs. 29–33). The spindle drawn was 60 μ in length. After the approximation of the chromosomes into pairs the spindle broadens; the fibers become less conspicuous, and finally disappear, leaving a group of irregularly arranged chromosomes within the now much reduced nuclear space (figs. 43–45). Meanwhile the chromosomes migrate to the center of the nucleus, and soon the second set of fibers is formed (fig. 46). At first these are restricted to the region in which the chromosomes are situated; as the chromosomes move to the poles, the whole nucleus becomes

pervaded by fibers radiating from irregular centers (fig. 51). In the egg of *Abies* there is an excessive development of intranuclear fibers. It seems reasonable to suppose that they originate from cytoplasmic material which has entered the nucleus during its growth period, and which may be differentiated into the fibrous form under physiological conditions not yet determined.

The slender filaments pervaded by small granules are scattered throughout the greater part of the nucleus. They are most definitely organized at the time when the spindle fibers are most conspicuous (figs. 27, 33, 42). When the fibers disappear, the filaments become disorganized, resulting in a granular mass (figs. 43, 46); when the spindle fibers appear the second time, the whole nucleus becomes more or less fibrous (fig. 51); when the daughter nuclei are formed, these bodies are not included, but form a matrix for the nuclei (figs. 49, 50). We may conclude that these filaments also are cytoplasmic, resembling the spindle fibers in nature, and becoming differentiated under similar conditions.

Pairing of chromosomes in fertilization

The succession of events which occur in connection with fertilization and the first division of the zygote has been traced not only by a consideration of the stages in the approximation and redistribution of chromatin bodies, but also by tracing parallel series of changes in the size of the nucleus, in the modifications of the deeply staining food bodies, and in the formation and dissolution of spindle fibers. A study of the chromatin, involving as it does the union of the male and female elements and distribution in the daughter nuclei, is of primary importance. Emphasis has been given first to a study of the related phenomena, already described, thereby eliminating, in so far as is possible, the possibility of a misinterpretation of the order of events.

The approximation of male and female nuclei has been described for a number of conifers. In general the process as found in *Abies* agrees with that of these descriptions. A few features may be noted. No cytoplasm could be detected adhering to the male nucleus as it approached the egg nucleus. There is a great disparity in the sizes of the pairing nuclei; that of the egg, as shown in fig. 19,

is 120 μ by 80 μ, while the male nucleus is 45 μ by 15 μ. The membranes of the nuclei are resorbed at the place of contact, and the contents of the male nucleus pass into the interior of the female nucleus, thereby leaving a protuberance containing very little cytoplasm.

In *Abies* the chromatin could not be detected definitely until the formation of two groups in the micropylar end of the egg nucleus takes place. While the groups are still distinct, the individual chromosomes become separate (fig. 28), each group containing the haploid number of chromosomes. As the two spindles unite, the chromosomes become paired (figs. 21–33); at first the individuals of a pair approximate side by side (figs. 31, 32); soon they twist about one another and jointly loop into the form of a C (figs. 30, 32, 33). The chromosomes are very large, in some cases exceeding 20 μ in length. There is abundant evidence that this is a pairing, not a longitudinal splitting of chromatin elements. First, the number of pairs is haploid. This is the number which would necessarily result from a pairing of the double number of chromosomes already present; a splitting would, of course, result in $2x$ pairs. Also, the twisting of the chromosomes about one another is identical with their behavior in what is generally regarded as a pairing during the prophase of the first reduction division. Moreover, there follows a transverse segmentation. If the diploid number of chromosomes should undergo two divisions, one longitudinal and one transverse, an $8x$ number of chromosomes would necessarily result. The facts cannot be explained by the supposition that there is a longitudinal split; they are readily explained by regarding this paired appearance as a true pairing.

The segmentation.—The bending into C or V-shaped forms is followed by a segmentation of each component of the pairs; in other words, a transverse fission at the angle of the bent chromosomes (figs. 34, 40). The resulting $4x$ daughter segments are approximately 10 μ in length, or one-half the length of the pairs before and during the looping process. At first the segments remain more or less twisted about one another (figs. 34, 37, 41, 42), and for some time retain a paired relation (figs. 43, 45). They may be in the form of X's, or V's, or parallel rods. At the time when

the second set of spindle fibers begins to be differentiated, the $4x$ number of chromosomes are indiscriminately intermingled (figs. 46–48). Half the number pass to each pole to form the daughter nuclei.

The chromosome count.—Repeated chromosome counts in the sporophyte and gametophyte confirm one another in fixing the x and $2x$ numbers for *Abies balsamea* as 16 and 32. The individual chromosomes which appear during the prophase of the division in the central cell are shown in figs. 8 and 9. The count is 16. The division of the body cell in anaphase gives 39 segments. A reconstruction of parts separated by the microtome knife results in a count of 32, or 16 passing to each pole. At the time of approximation of the chromosomes in the egg, there are 16 pairs (figs. 29–33). When segmentation takes place, 32 pairs of segments are present (figs. 34–40). In the nucleus represented in figs. 43–45, there are 72 chromosome pieces; figs. 46–48 show 63 almost complete chromosomes, besides a number of ends. Undoubtedly we have in each case the $4x$ number, or 64 chromosomes.

The daughter nuclei.—During telophase the chromatin strands remain remarkably distinct (figs. 49–52). They elongate greatly, and become irregularly looped (figs. 50, 52). It would seem that each is in contact with the periphery somewhere throughout its length. Contraction is followed by an increase in the size of the nuclear space; the latter is accompanied by a vacuolization of the chromatin (fig. 55). The nuclear outline is still lobed, the lobes corresponding to the loops of chromatin. The nuclear membrane forms late. As the nucleus continues to enlarge, the chromatin becomes still more discontinuous, but the outline of the strands may still be readily traced.

It is to be noted that of all the material which was inclosed by the membrane of the egg nucleus, only the chromatin is included in the newly organized daughter nuclei. The large vacuolate darkly staining bodies, the filaments pervaded by granules, and the fibers are all excluded when the membranes inclose the daughter nuclei. We may conclude that these materials, although they may be found within the nuclear membrane, are not essentially nuclear and are not directly concerned in mitosis. They are, at most,

cytoplasmic inclusions within the nucleus. The chromatin is the fundamental nuclear substance.

Discussion

The ventral canal cell.—The general tendency among the Coniferales is toward the reduction of the ventral canal cell. In the Abietineae a cell is cut off by a cell wall; in the Taxineae and Cupressineae, as groups, a ventral nucleus is formed, but no cell is organized; while in *Torreya* (**15**) there is no ventral cell, the nucleus of the central cell becoming the egg nucleus. In *Abies* the nucleus of the ventral canal cell functions as an egg. In *Pinus Laricio* (**3**, p. 278), "while the ventral canal cell nucleus usually disappears soon after it is formed, in some cases it persists, and its nucleus becomes as large as that of the oosphere, passing through a similar developmental history. New support is thus given to the theory that the ventral canal cell is the homologue of the egg."

NICHOLS (**21**) describes (fig. 90) "two nuclei resulting from the division of the ventral canal cell nucleus" in *Juniperus*. The ventral canal cell "is fairly persistent in *Tsuga* (**20**). When division is complete, its nucleus is equal in size and similar in structure to the nucleus of the egg, and for some time shows the same stages of development."

The most extreme development recorded is in the case of *Thuja*, described by LAND (**14**). "A number of the writer's preparations of *Thuja* lead him to believe that both the ventral nucleus and the egg, in the same archegonium, may be fertilized. In fig. 17 the proembryo is well advanced, while the ventral nucleus has formed a group of four cells. Another preparation shows eight cells with indications that walls are soon to appear. The probability of such a fertilization is strengthened by finding occasionally in the same ovule embryos growing upward into the nucellus, as well as downward into the endosperm" (p. 224). These facts and those already described for *Abies* remove any doubt that the ventral canal cell is potentially an egg.

The cytoplasmic "mantle" about the egg nucleus is present in most species of Coniferales. NICHOLS (**21**) describes it in *Juniperus* as follows: "The mass of cytoplasm and starch derived from the

male cell gradually surrounds the conjugating nuclei so that there is never any possibility of mistaking the fusion nucleus for an unfertilized egg nucleus." And NORÉN (**22**) states: "Nachdem die Kopulation der Kerne erfilgt ist legt sich das Plasma der Spermazelle und deren Stärke wie ein Mantel um die beiden Kerne herum." The description is similar for *Taxodium* (**4**), *Torreya* (**15**), *Sequoia* (**16**), and *Thuja* (**14**). In *Ephedra* (**13**), a dense cytoplasmic mass develops about the egg nucleus and extends downward in the cytoplasm of the egg. In *Abies* a finely granular cytoplasmic layer develops about the egg nucleus during its movement toward the center of the egg (figs. 7, 14). This area extends along the path of the nucleus in the form of a short streamer. The male nucleus penetrates the mantle, but there is no appreciable addition to its mass by cytoplasm accompanying the same (fig. 19). At the telophase of the first division, the excess material from the egg cytoplasm is added to the "mantle" (figs. 49, 50, 55).

The darkly staining bodies described in *Abies* as globular or irregularly shaped and vacuolate, according to conditions, have been variously interpreted. NICHOLS (**21**) writes: "In the egg nucleus frequently the entire chromatin content of the nucleus seems to have resolved itself into nucleoli and pseudo-nucleoli. Yet even after a study of a large number of preparations one is unable to formulate any satisfactory conclusions as to the nature of these structures." Describing the egg nucleus of *Taxodium*, COKER (**4**) says: "In addition to the reticulum and plastin nucleoli there are also present numbers of chromatin nucleoli." And LAWSON for *Libocedrus* (**17a**) states that "It is impossible to distinguish the true chromatin from the nucleoli and other irregularly shaped bodies which stained like chromatin, and seemed to be closely associated with the latter." These bodies seem to resemble very much the karyosomes which SHARP (**24**) has described in the resting nuclei of *Vicia Faba*. "They appear in connection with the chromatic network and resemble the latter in staining quality. They seem to represent an elaboration product of a process actively going on during rest." A study of *Abies* has led to the conclusion that the darkly staining bodies are storage materials derived from the cytoplasm.

A cytological study of fertilization in conifers has been made for a number of species: CHAMBERLAIN, *Pinus Laricio* (3); BLACKMAN, *Pinus silvestris* (2); Miss FERGUSON, *Pinus* (6); MURRILL, *Tsuga canadensis* (20); NORÉN, *Juniperus* (22); and NICHOLS, *Juniperus* (21). "After the male pronucleus is within the oosphere nucleus the chromatin of the two pronuclei appears as two distinct masses in the spirem stage" (3). "Es scheint als würde jede der beiden Chromatingruppen zuerst ihre eigen Kernspandel ausbilden, die sich dann zu einzigen vereinigen" (22). On the fibers "the long bent and twisted chromosomes appear" in *Tsuga* (20). Miss FERGUSON (6) states: "When the chromosomes are being oriented at the nuclear plate, the maternal and paternal elements can no longer be distinguished." The number of chromosomes at this stage was found to be $2x$. No count is recorded during the phase of pairing (or splitting, as it has generally been regarded). Miss FERGUSON'S figures confirm what has been described for *Abies*. Her figs. 236 and 237 may be compared with figs. 29–33; her fig. 238 with figs. 34–39; and her fig. 241 with fig. 51. As illustrated by diagram *B*, a number of stages in the process of fertilization have not been described heretofore. It is not surprising that, without these stages and not having the chromosome count throughout, the pairing should be interpreted as a longitudinal split, and that evidence of segmentation should not be found. Because of the complete series found in *Abies* and the extreme size of the chromosomes, it has been possible to discover the facts which center about the pairing, followed by the transverse segmentation.

Stages in fertilization.—A study of the union of egg and sperm in plants and animals makes it evident that there are several phases in the process of fertilization. The primary phase is illustrated by Uredineae. Here the fusion is evidently incomplete during the binucleate stages. "In the young aecidium the nuclei become paired and divide together in very close association. The teleutospores in the young state are binucleate, but when mature become uninucleate by the fusing of the two paired nuclei" (1). It is only after many separate but simultaneous divisions of the pairing nuclei that this second phase of the process is accomplished. HARPER (8) believes that bivalent chromosomes are formed in

Ascomycetes. "The time and degree of the combination of the sexual chromosomes is a variable matter. If the prochromosomes can remain in one nucleus with the double chromosome number, or in two distinct nuclei through part or all of the sporophyte generation, it is also possible that they may combine in one nucleus into bivalent chromosomes, and maintain their identity in this

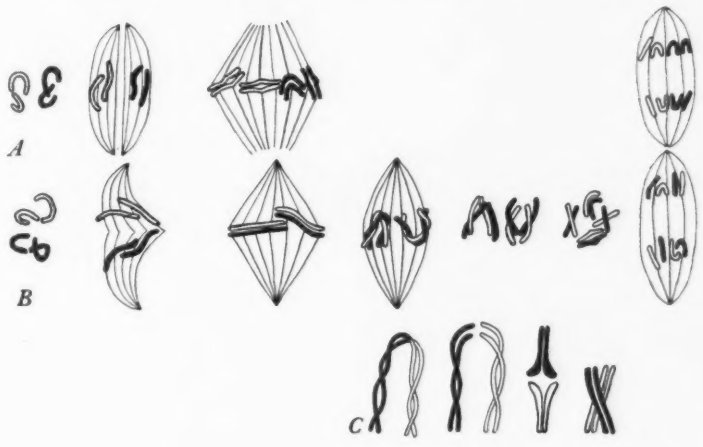

FIG. 1

Diagram *A*.—An interpretation of fertilization in some animals and in *Pinus*, according to the accounts heretofore recorded.

Diagram *B*.—An interpretation of the phenomena already described: the chromatin originating from the egg nucleus is shown in solid black, that from the male nucleus is outlined and barred; the argument upon which such an interpretation is based is included in the description given in the text; the facts of spindle formation are also indicated.

Diagram *C*.—A copy from GRÉGOIRE'S (7) "schéma de l'interprétation metasyndetique des tétrades-crois," as found in certain lower animals; compare fig. *B*.

condition through the sporophyte generation until a true reduction occurs in spore formation." In the well known case of *Cyclops*, studied by HAECKER, the parental chromosomes do not mingle, but persist as individuals and maintain their separation into two groups through several cell generations after "fertilization." We may consider the union of egg and sperm as consisting of three stages: (1) the two nuclei enter the same cytoplasmic mass; (2) the two

groups of chromosomes enter the same nuclear membrane, but retain their former grouping; and (3) the chromosomes pair. The first is illustrated by the paired nuclei in Uredineae; the second by the chromatin groups during the first divisions of the *Cyclops* embryo; the third takes place soon after the fusion of the egg and sperm in *Abies*. It seems altogether probable that the chromosomes do not actually pair until the prophase of the reduction division in such animals as *Cyclops*. There is a striking similarity between the pairing process as described in *Abies* and that concerned with tetrad formation in some animals (compare diagram *A* with diagram *C*). To what extent we are justified in suggesting that the processes are identical and that they are both concerned with the pairing of corresponding chromosomes from the egg and from the sperm, only further research can definitely determine.

Relationships

Abies, as compared with *Pinus*, shows a number of primitive characters:

1. The male gametophyte: (*a*) an excessive polar ("prothallial") tissue; (*b*) the equality of the male nuclei; both may function.

2. The female gametophyte: (*c*) the large number of neck cells; as many as five tiers (MIYAKI **19**); (*d*) the persistence of the ventral canal cell; its nucleus may function as an egg nucleus.

3. The ovulate strobilus and ovules: (*e*) the almost complete separation of scale and bract; (*f*) the development of a rudimentary pollen chamber; (*g*) the comparatively free integuments.

4. The staminate strobilus: (*h*) the staminate strobili are borne on ordinary branches in the axes of ordinary leaves.

5. The arrangement of leaves: (*i*) the spiral arrangement of leaves on ordinary branches (THOMSON **25**; LLOYD **18**).

6. Vascular anatomy: (*j*) the general absence of ray tracheids (THOMPSON **26, 27**), which in *Pinus* are present in the mature wood, but absent in the seedling and strobilus axis.

It may be noted, however, that resin canals are not found in the woody axis of the *Abies* stem except as traumatic responses (JEFFREY **11**). JEFFREY states that the presence of resin ducts is an ancient character which has persisted in *Pinus*. "On account

of the reduced foliage of the abietineous conifers, this [that is, resinous secretion] was a very serious drain on the assimilatory apparatus. Gradually the more economical tendency arose of forming resin passages in the case of need only." So regarded, *Pinus* would be more primitive than *Abies*. Whether or not this argument is sufficient to overbalance the numerous ancient characters of *Abies* previously tabulated is a matter of judgment which we do not presume to decide.

Many of the foregoing characters are such that they tend to relate more closely the two ancient groups of Coniferales, the Abietineae and the Araucarineae.

Summary

1. *The male gametophyte.*—The polar ("prothallial") cells may divide mitotically. The body cell divides to form the male nuclei while within the spore coat. Under favorable conditions a "prothallial" cell may develop as an antheridial cell, a biantheridial gametophyte resulting. The male nuclei are equivalent; one fuses with the egg nucleus and frequently the other fuses with the ventral canal cell nucleus.

2. *The ventral canal cell and ventral proembryo.*—The ventral canal cell nucleus breaks through its wall into the egg cytoplasm, enlarges, and fuses with one of the male nuclei. A ventral proembryo is formed by two successive divisions.

3. *The egg nucleus.*—The egg nucleus enlarges to 60 times its original volume. At the time of fertilization (fig. 28) irregular, darkly staining, vacuolate masses, slender filaments pervaded by small granules, spindle fibers, and chromatin are differentiated within the nuclear membrane. The chromatin is the fundamental nuclear substance; the other bodies are accretions gained during the growth of the nucleus and excluded from the nuclei of the proembryo.

4. *Fertilization and the first division.*—After fusion two chromatin groups appear at the base of the egg nucleus; in each $2x$ chromosomes become separate; the two original spindles unite; the chromosomes approximate to form x pairs; they twist the one about the other and become looped; each of the components of a pair

segments medianly, that is, at the apex of the loop; $2x$ pairs of segments result; these separate to form $4x$ chromosomes; a new spindle is formed and $2x$ chromosomes pass to each pole.

5. Fertilization may be regarded as having three phases: (1) sex nuclei enter a common cytoplasm; (2) the two groups of chromosomes enter a common nuclear membrane; (3) the chromosomes approximate in pairs. The first phase may be prolonged, as in Uredineae; the second may be prolonged, as in some animals; or the three phases may follow one another in rapid succession, as in *Abies*. Attention is drawn to the similarity existing between the phenomena connected with pairing in *Abies* and tetrad formation in animals. It is suggested that they may be like processes occurring at different stages of the life history.

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UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES XVI–XX

FIGS. 1–5.—Pollen grains: male gametophyte.

FIG. 1.—Division of polar cell; ×510.

FIG. 2.—Biantheridial gametophyte; ×510.

FIGS. 3–5.—Division of body cell; ×865.

FIG. 6.—Central cell and two neck cells; ×510.

FIG. 7.—Ventral canal cell and egg nucleus; ×510.

FIGS. 8, 9.—Mitosis of nucleus of central cell; ×865.

FIG. 10.—An archegonium: egg nucleus, ventral canal cell with wall broken and escaped nucleus in the cytoplasm of the egg; ×85.

FIGS. 11, 12.—Nucleus of ventral canal cell escaping.

FIG. 13.—Egg nucleus near a male nucleus; ventral canal cell nucleus, and near by the other male nucleus and stalk nucleus.

FIG. 14.—Detail of egg nucleus of fig. 10.

FIG. 15.—Two archegonia, one showing fertilization of both egg and ventral canal cell nucleus; ×85.

FIG. 16.—Divisions following the two fusions; ×85.

FIG. 17.—Ventral canal cell nucleus: a male nucleus and the stalk nucleus in contact; ×510.

FIG. 18.—Fusion nucleus resulting from union of ventral canal cell nucleus and male nucleus; ×510.

FIG. 19.—Egg nucleus and male nucleus in contact; ×510.

FIG. 20.—Egg and male nucleus in contact (see detail in fig. 19): the ventral canal cell nucleus as described for fig. 18; ×510.

FIG. 21.—An archegonium showing the egg nucleus, ventral canal cell nucleus, four male nuclei, a stalk nucleus, and two pollen tubes; ×510.

FIG. 22.—Postion and relation of ventral proembryo and proembryo proper; ×510.

FIGS. 23–26.—Detail of division following the fertilization of the ventral canal cell nucleus; ×865.

FIG. 27.—Nucleus of the fertilized egg; ×510.

FIG. 28.—Nucleus of the fertilized egg: two groups of chromosomes; ×510.

FIGS. 29–33.—Pairing of chromosomes; ×865.

FIGS. 34–40.—Segmentation of chromosomes; ×865.

FIGS. 41, 42.—Paired segments; ×865.

FIGS. 43–45.—Chromosome segments intermingling, still somewhat paired; ×865.

FIGS. 46–48.—Chromosomes starting to the poles; ×865.

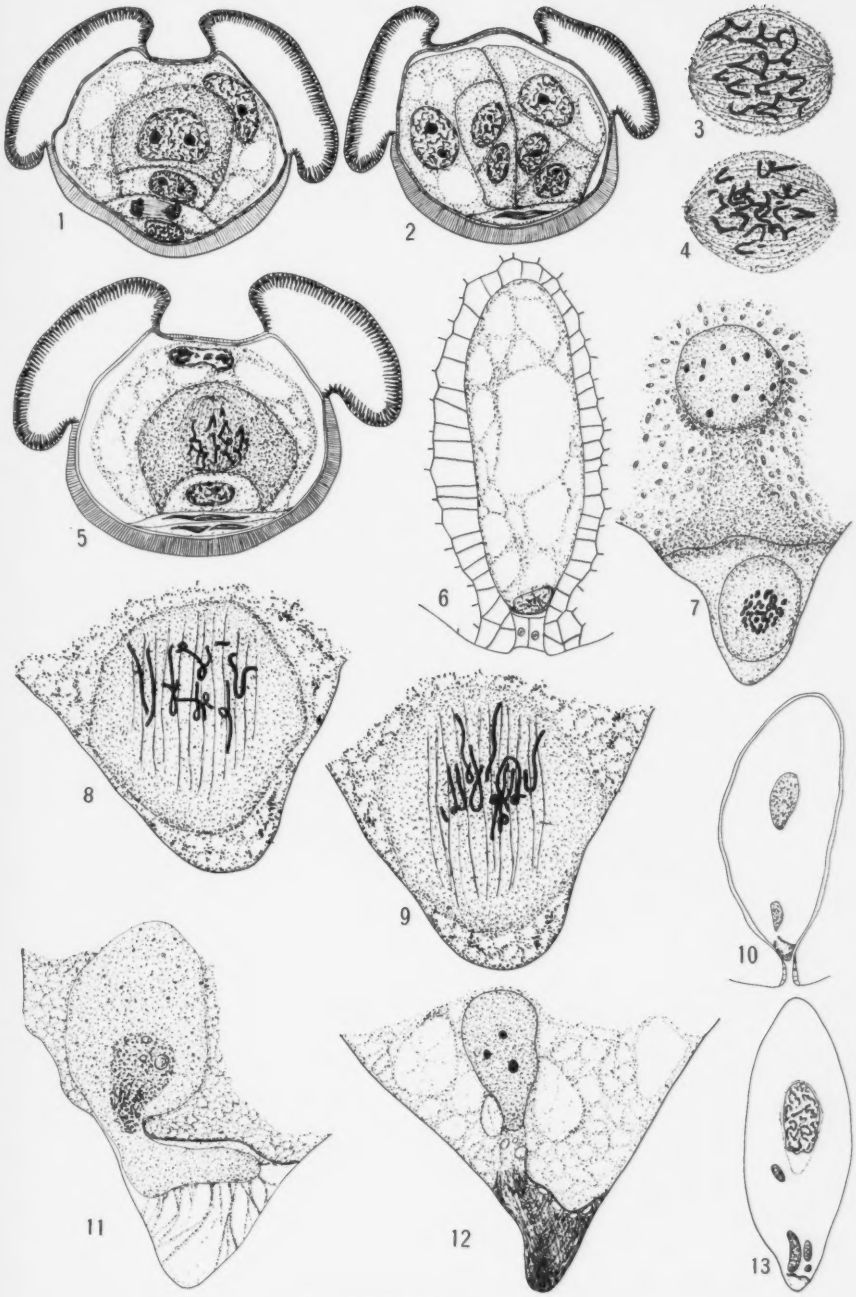
FIG. 49.—Early telophase of first division; ×865.

FIGS. 50, 52, 55.—Late telophase of first division; ×865.

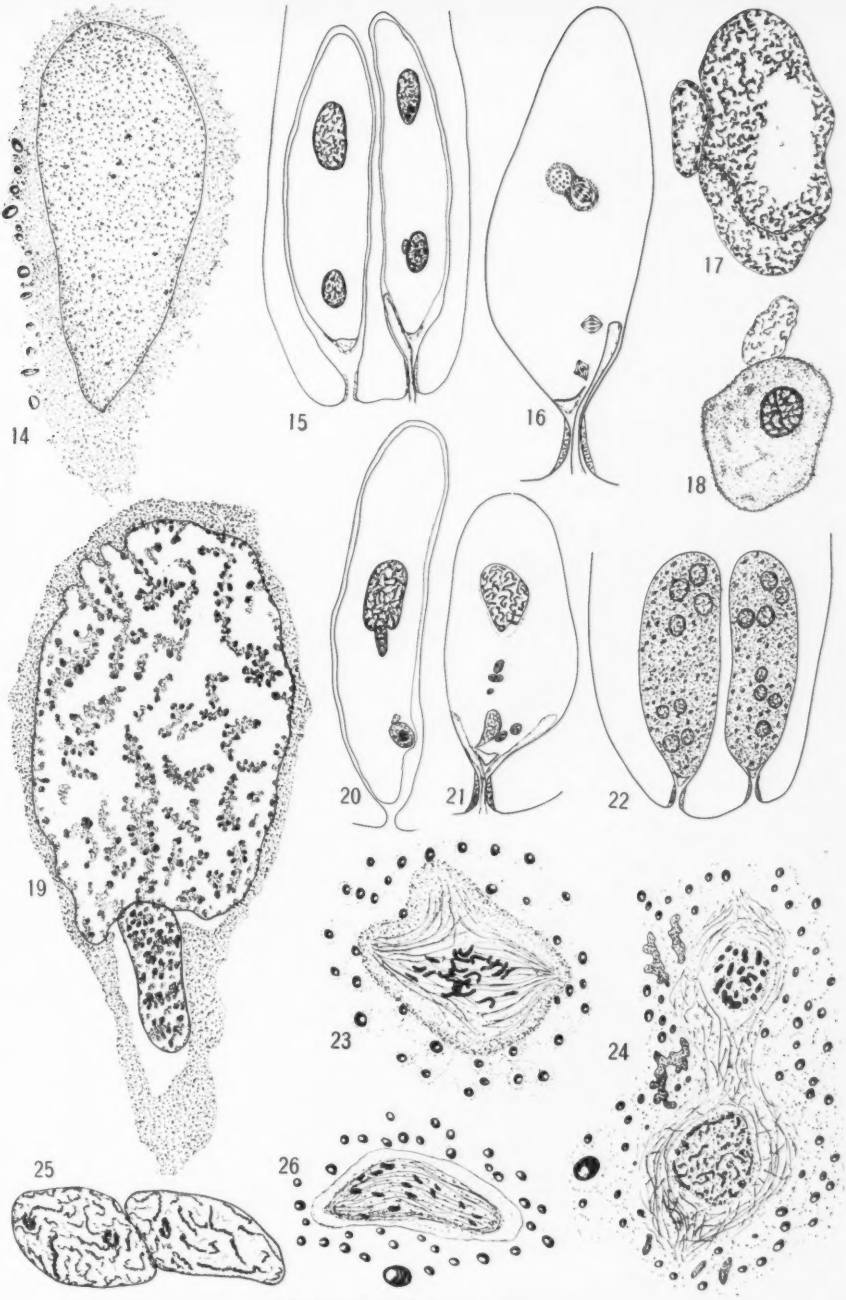
FIG. 51.—Anaphase of first division; ×865.

FIG. 53.—Resting stage of nucleus from ventral proembryo; ×865.

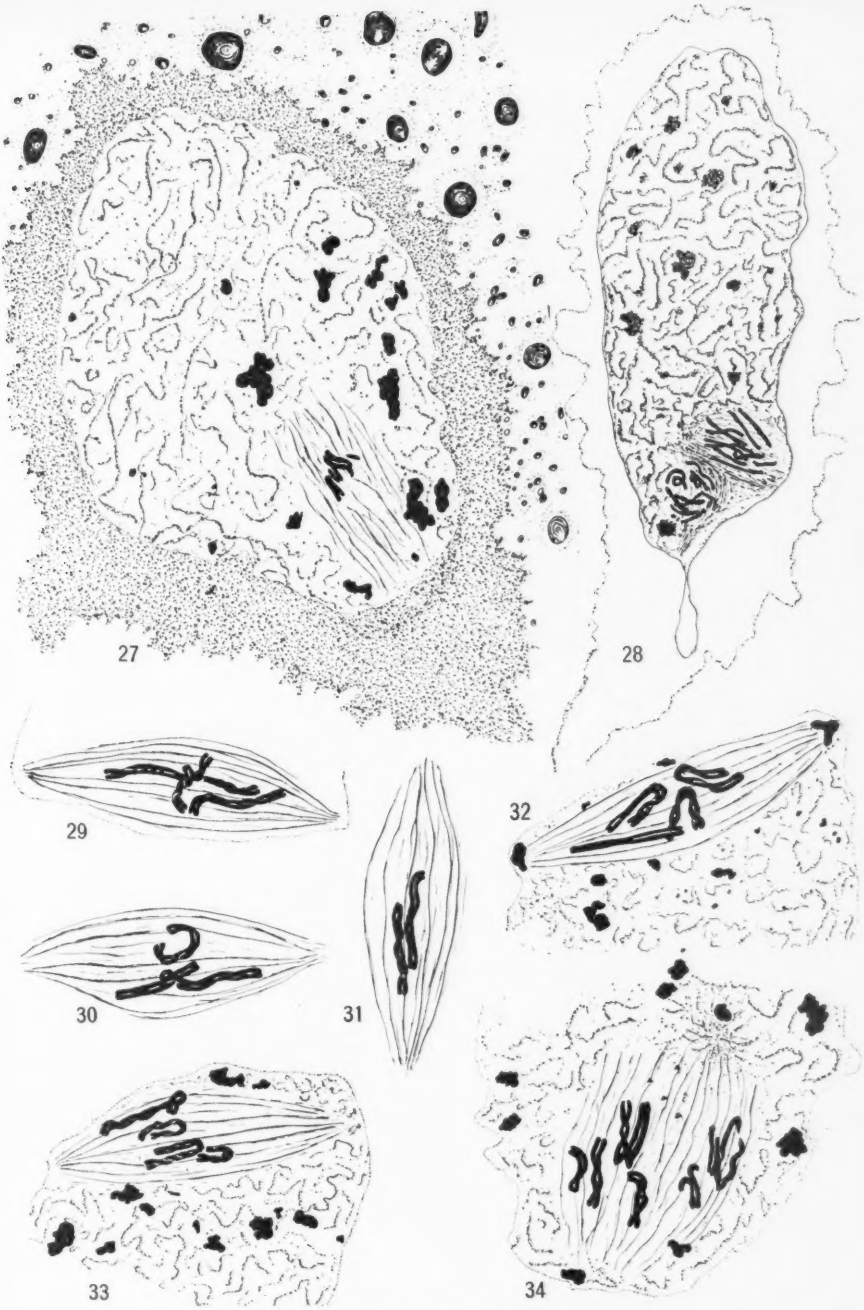
FIG. 54.—Resting stage of nucleus of the proembryo; ×865.



HUTCHINSON on ABIES



HUTCHINSON on ABIES



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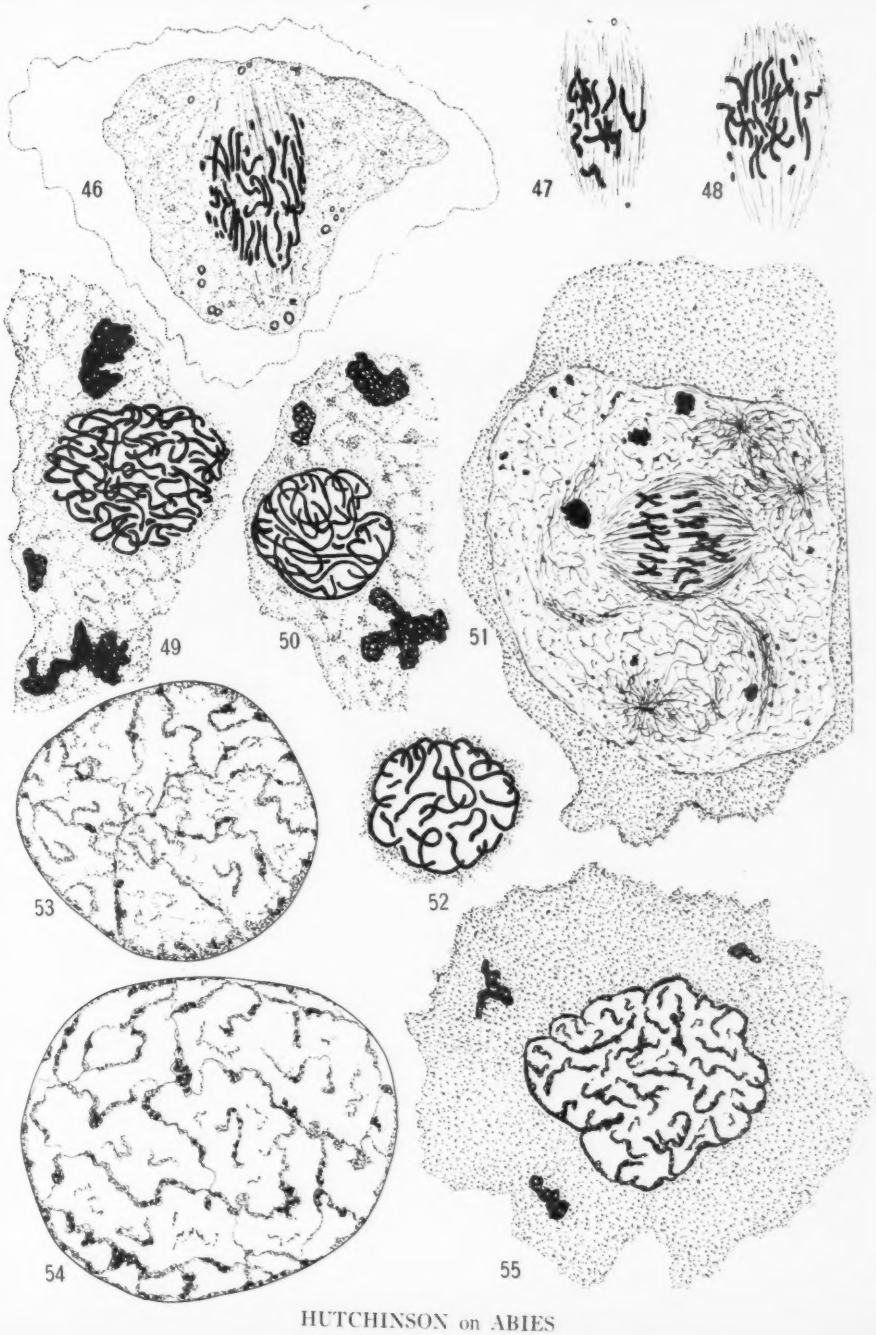

HUTCHINSON on ABIES

THE SIZE OF KELPS ON THE PACIFIC COAST OF NORTH AMERICA

T. C. FRYE, G. B. RIGG, AND W. C. CRANDALL

(WITH TWO FIGURES)

Introduction

The personal observations of the authors on the size of kelps have covered much of the west coast of North America from Cedros Island on the coast of Mexico to the Shumagin Islands on the coast of western Alaska.

The work of FRYE has been done during ten summers spent on Puget Sound, during several of which he has been director of the Puget Sound Marine Station at Friday Harbor, Washington, and one summer (1913) during which he was in charge of the expedition sent to southern Alaska by the United States Bureau of Soils for the purpose of investigating the kelps as a source of potash fertilizer.[1] The investigations of that summer included a careful examination of the coast from Dixon Entrance to Juneau (not including the west coast of Baranof Island), together with observations on kelps at a number of points along the coast of British Columbia where opportunity offered on the way to Alaska in May.

The observations of RIGG cover six summers in the Puget Sound region, portions of three of which were spent at the Puget Sound Marine Station, and portions of two of which were spent in making a survey of the kelp beds of the Puget Sound region for the United States Bureau of Soils as a part of its investigation of those kelps as a source of potash fertilizer. RIGG'S Alaskan observations were made during the summer of 1913 when he was in charge of the United States Bureau of Soils expedition to western Alaska for the investigation of the kelps of that region as a source of potash

[1] All of the kelp investigation expeditions of which the writers of this paper were in charge were a part of the general investigation of the fertilizer resources of the United States conducted by Dr. FRANK K. CAMERON of the United States Bureau of Soils.

fertilizer. A few incidental observations were made on kelps along the British Columbian coast and in southern Alaska on the way through that territory in May. Stops were made at Dixon Harbor, just north of Cape Spencer, and at Yakutat. No stop was made from Yakutat to Prince William Sound, but from this sound to the Shumagin Islands (including Cook Inlet and Kodiak Island) a reconnoissance survey was made. A careful examination of the coast was made at all points where conditions of weather and tides would permit.

The work of CRANDALL covers the coast from Cedros Island, Mexico, to Cape Flattery, Washington. It was done by him as biologist at the Scripps Institution for Biological Research and under appointments of the United States Bureau of Soils in 1911, 1912, and 1913 to investigate the kelps of the region as a source of potash fertilizer.

The maximum size of kelps on the Pacific coast of North America has been a matter of interest ever since the beginning of botanical investigation in the region. Naturally a careful watch for large kelps was kept on these expeditions and frequent soundings in kelp beds were made. No specimens of *Nereocystis* or *Macrocystis* were found that at all approached in length the figures given for these species by the earlier writers. The figures that had been reported for the length of *Alaria fistulosa* were, however, practically corroborated, and the width of that species was found to be much greater than had been reported.

Macrocystis

Macrocystis pyrifera has been reported (without locality) by KJELLMAN (**7**) to reach a length of 200–300 m. It has been reported by FITZROY (**3**) that it grew about the Falkland Islands in 30 fathoms of water, and by CAPTAIN COOK (**1**) that it grew at Kerguelen Island in 24 fathoms of water and that he feels warranted in saying that it reaches a length of 60 fathoms.

HARVEY quotes HOOKER as having calculated this species to reach a length of 700 feet (213 m.), and states that BORY ST. VINCENT attributes to specimens a length of 1500 feet (457 m.). HOWE (**6**) reports measurements of *Macrocystis pyrifera* and *M. integrifolia*

from Peru. In regard to the size of the first species he quotes (p. 64) a field note of the collector (Dr. ROBERT COKER) as follows: "The largest piece measured 10 m. and the entire single cluster weighed 30 lbs." He refers to the second species (p. 61) as "the short plant (2–3 m. long) that grows gregariously on surf-swept rocks with densely intertangled rhizomatous holdfasts. . . . ." BURD (**2**) found *Macrocystis* plants varying in weight from 27 to 300 pounds. The largest specimen reported from the Puget Sound region is 40 feet in length (RIGG **12**).

This species was not found growing in the territory covered by the western Alaskan expedition, but beds of it were found by the southeastern expedition. The deepest water in which it was found growing was 12.5 m. Where the plants were growing in water of this depth, the longest portion of an attached plant floating at the surface was 13.8 m. If this plant rose from the bottom at an angle of 45°, the under-water portion would be 17.3 m. long, and the whole would be 31.1 m. It seems likely that it rarely if ever reaches a length of 38 m. in Alaska.

The longest *Macrocystis* plant found on the Californian coast measured 45.7 m. Many are only 9–13 m. long. This species with a definite holdfast has been found by the writers growing in water varying in depth from $2\frac{1}{2}$ to 14 fathoms. When it grows in shallower depths the holdfast is more like a rhizome. A single specimen of this plant has been found on the Californian coast that weighed 136 kg. A specimen collected at Santa Barbara, California, was 23 m. in length and weighed 22 kg. Another one collected at the same place was 25 m. long and weighed 37 kg. The deepest sounding made in a *Macrocystis* bed was 14 fathoms. This was on the Californian coast. The deepest sounding made in Alaska was 7 fathoms.

Pelagophycus

Pelagophycus porra has been found 45 m. in length on the Californian coast (fig. 1). It has not been found in the Puget Sound region or in Alaska. The deepest sounding made in *Pelagophycus* beds was 20 fathoms. BURD (**2**) found that these plants varied in weight from 16 to 71 pounds.

Nereocystis

Statements of the length of *Nereocystis luetkeana* in various localities are shown in table I.

TABLE I

Observer	Locality	Date	Depth reported	Meters	Part measured
Mertens	Alaska	1829	45 fathoms	82.3	Stipe only
Harvey	Without locality	1852	340 feet	103.0	Whole plant
Ruprecht	Alaska	1852	250 "	76.2	" "
Kjellman	Without locality	1897	100 m.	100.0	" "
MacMillan	British Columbia	1899	80 feet	24.4	" "
MacMillan	" "	1901	100 "	30.5	" "
Saunders	Alaska	1901	70 "	21.3	" "
Frye	Puget Sound	1906	21 m.	21.0	" "
Setchell	California	1908	41 "	41.0	" "
McFarland	"	1912	100 feet	30.5	" "
Rigg	Puget Sound	1912	72 "	21.9	" "

SAUNDERS (**15**) thinks that MERTENS' statement is "probably not true," since he (SAUNDERS) "has measured many fully developed plants on the California, Oregon, and Washington coasts, as well as on the Alaska coast, and has never found one exceeding the above figures" (70 feet). FRYE (**4**) has indorsed SAUNDERS' view. SETCHELL (**16**) sees a possibility that the "45" in MERTENS' statement is a "misprint . . . . for 15, which, from all experience seems likely." He prefaces this, however, with the suggestion that MERTENS' statement "must have been made with care, as are his statements in general." He also quotes RUPRECHT, who had found specimens 25 feet long on the Californian coast, but had added "that according to trustworthy natives in the employ of the N. A. Company at Fort Ross, it reaches a length ten times greater in the vicinity of Sitka and the Aleutian Islands." SETCHELL also says that in his observations from Kodiak Island, Alaska, to California he did not find any specimens that approached the dimensions reported by MERTENS and RUPRECHT, but adds "Off the entrance to Yakutat Bay, Alaska, while at anchor during a fog I saw soundings taken close to and among *Nereocystis* plants showing that the solid portions of the stipe were 10–12 fathoms in length. Altogether the plants thus observed must have been 45–50 m. in length." SETCHELL's report of 41 m. above is based on a specimen

FIG. 1.—*Pelagophycus porra*, or elk kelp.—From Report no. 100, Bureau of Soils.

that he paced at Carmel Bay, California. MACMILLAN (9) expresses the opinion that the length stated by KJELLMAN "is not at all excessive." MCFARLAND (8) says: "I have been unable to find individual plants of *Nereocystis* in the region examined by me which attained anything like the maximum dimensions given by KJELLMAN, MERTENS, SETCHELL and GARDNER, and MACMILLAN. Specimens up to 100 feet in length are met with."

It should be noted that RUPRECHT's statement was based on mere hearsay. KJELLMAN (7) does not cite any measurements in support of his statement. MERTENS' (11) statement has never been confirmed by measurements. There is practical agreement in the statements by SAUNDERS (15), FRYE (4), and RIGG (12, 13). Longer kelps than those found by the last three observers were reported by MACMILLAN (10), SETCHELL (16), and MCFARLAND (8).

Not a single specimen has ever been found by the writers of this paper that reached 40 m. in length, nor has any evidence been obtained by them from soundings that plants reach this length in any of the beds examined. The largest specimen of *Nereocystis* measured on the southern Alaskan expedition was 20.7 m. This was at Point Davidson on Annette Island. The longest specimen of this species measured on the western Alaskan expedition was 18.9 m. This was at Resurrection Bay on the Kenai Peninsula. Many statements were made to the writers about extremely large kelps, but when the beds were visited, these large specimens could not be found. The longest lamina found by our expeditions is 780 cm. The greatest width of lamina found is 20 cm. The length of a pneumatocyst found at Yakutat was 462 cm. All measurements of kelps at Yakutat were from drift specimens. None were seen growing. The region was visited in May, which is too early for the new crop of kelp there. The maximum circumference of bulbs measured on our expeditions is 453 mm. This specimen was found at Danger Bay on Afognak Island. Other bulb circumferences measured were 425 mm. at Meares Passage, 367 mm. at Yakutat, 365 mm. at Sand Point, and 350 mm. at Resurrection Bay.

MCFARLAND (8) has found the weight of fresh *Nereocystis* plants on the Californian coast to vary from 43 to 76 pounds. BURD

found a maximum weight of 56 pounds at the season at which the sample was taken (fall). One of us (RIGG **12, 13**) has found the weight of the fronds and pneumatocyst to be 18–35 pounds on Puget Sound. The maximum weight found by our expeditions in Alaska was 55 kg. This included the fronds and 210 cm. of the pneumatocyst. The fronds alone weighed 49 kg. This specimen was collected at Resurrection Bay. The same portions of specimens collected at other points weighed as follows: Smith Island, 24 kg.; Sand Point, 16 kg. The slender portion of a stipe collected near Seattle, Washington, was found by the writers to weigh 87 gm. per meter. A similar piece collected at Sand Point, Alaska, weighed 227 gm. per meter. A holdfast at Sand Point weighed 3.4 kg.

A summary of the measurements of the largest *Nereocystis* plants found by the writers is given in table II.

TABLE II

Locality	Total length (m.)	Length of fronds (m.)	Diameter of bulb (mm.)	Weight of plant (kg.)
Pacific Grove, Cal., 1913.....	34.7	1.8	93	7.0
Pacific Grove, Cal., 1913.....	36.5	3.6	137	13.6
Pacific Grove, Cal., 1913.....	38.4	1.8	100	7.5
Friday Harbor, Wash., 1911....	21.9	.....	.....	.....
Seward, Alaska, May 1913.....	19.0	7.9	116	55.4
Yakutat, Alaska, May 1913.....	.....	.....	120.5	.....
Sand Point, Alaska, July 1913...	13.7	3.3	113.0	16.2
Pt. Davidson, Alaska, May 1913.	20.6	5.4	.....	.....
Meares Passage, Alaska, July 7, 1913.....	21.2	.....	.....	.....

The following soundings include the deepest ones made by the writers in beds of *Nereocystis:* Resurrection Bay, Alaska, 5 fathoms; Kodiak Island, Alaska, 6 fathoms; Danger Bay, Alaska, 6.5 fathoms; Pacific Grove, California, 9 fathoms.

Alaria

The other kelp forming large beds in Alaska is *Alaria fistulosa* (fig. 2). The maximum width mentioned by SETCHELL and GARDNER (**17**) is 1 m. and the maximum length is 25 m. The number of sporophylls is given at about 200.

FIG. 2.—*Alaria fistulosa:* general appearance of a wide-leaved plant.—From Report no. 100, Bureau of Soils.

Specimens collected by GRIGGS and RIGG at Anchor Point, Cook Inlet, measured as follows: length 13 m., 21 m., 22 m., 18 m.; width 232 cm., 175 cm., 170 cm., 123 cm., respectively. The first of these specimens had 220 sporophylls, the largest of which measured 65 cm. in length and 84 mm. in width. The width of the midrib was 53 mm.

All of these plants were badly frayed at the tip, a great deal of material evidently having been worn off by the violence of the tidal currents. Regeneration from the base seems to be continuous throughout the life of the individual in this species. It is thus impossible to say whether these specimens had at any time been longer than they were when collected.

The weights found by our expeditions for portions of the fronds of *Alaria fistulosa* of the sizes given are shown in table III.

TABLE III

Locality	Length (m.)	Width (cm.)	Weight (kg.)
Cook Inlet, Alaska	19.0	170	8.1
" " "	18.5	175	9.8
Red Bay, "	19.0	135	.....
Cook Inlet, "	14.0	132	7.1
Kodiak Island, "	15.0	25	0.9

The deepest sounding made in an *Alaria* bed was 5 fathoms (Middle Islands, Alaska).

Summary

1. The observations of the writers do not tend to confirm the earlier statements of the great length of *Nereocystis* and *Macrocystis*.

2. Their observations on *Alaria fistulosa* confirm earlier statements of its length. Its maximum width was found to be more than twice as great as reported in literature that has come to the attention of the writers.

UNIVERSITY OF WASHINGTON, SEATTLE,
AND
THE SCRIPPS INSTITUTION FOR BIOLOGICAL RESEARCH
LA JOLLA, CAL.

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NEW SPECIES OF ACHLYA AND OF SAPROLEGNIA[1]

A. J. PIETERS

(WITH PLATE XXI)

In the course of physiological work on *Saprolegnia* carried on during the past four years, there was occasion to make pure cultures of a large number of water molds. Altogether some 85 numbers were isolated and cultivated on flies or in artificial media or both. Among these forms were several that could not be induced to produce oogonia and which could not, therefore, be referred to any species. The author is of the opinion that in some cases such forms have completely lost the power to produce oogonia and that they should be described and named as new species, the diagnoses to rest on physiological rather than on morphological bases. However, his experience with some of these forms shows that it will be well to be cautious in drawing conclusions. In the case of a variety of *Saprolegnia monoica* to be described, the form was in cultivation for 16 months, on flies and in various media, without any sign of oogonia being produced. Later, when just the right combination of conditions was presented, oogonia were produced.

Another species, to be described as *S. Kaufmanniana*, produced oogonia sparingly on flies, many cultures not showing a single oogonium. In this form also a number of oogonia with oospores and antheridia were produced in a certain strength of haemoglobin solution, but in no other medium. These experiences show that the production of sexual organs may depend on some special combination of conditions, differing doubtless for each form. One form, which has been studied for 18 months as no. 66 and which has been tested in every way in which any of the other forms have been tested, still refuses to produce oogonia, though yielding an abundant harvest of round single gemmae. These gemmae have the shape and size of oogonia, and are commonly borne laterally on short stalks just as oogonia are in such a species as *S. monoica*. In

[1] Contribution from the Botanical Laboratory of the University of Michigan, no. 148.

fact, when these gemmae first form, the observer is certain that young oogonia are being produced, but in no case have oospores or antheridia been observed, though hundreds of cultures have been examined. It is possible that in this form these gemmae are nothing but arrested oogonia, and that, could we find the proper conditions, oospores and perhaps antheridia would be developed.

Certain details in regard to these and other tests will be presented in another paper; at present the writer wishes to describe a species of *Achlya*, which he has named *A. Klebsiana* in honor of Professor GEORG KLEBS. The naming of this species for Professor KLEBS seemed to the writer especially appropriate since at one time it seemed to be an exception to the rule laid down by KLEBS in 1899 that sporangia are formed only when the food supply is quickly and markedly decreased. Further study, however, showed that this apparent exception was a real and interesting proof of the correctness of KLEBS's statement. The experiments showed that while an abundance of food was present in the solution in which sporangia were formed, it was not available to the growing hyphae and consequently might as well not have been there. While working in Heidelberg the writer observed that a culture of *A. DeBaryana* Humphrey regularly produced sporangia in agar to which pea broth had been added. The sporangia were mostly borne on the large, vigorous hyphae that made a rapid growth immediately after a fresh plate of pea agar was inoculated. Later very many slender hyphae, which grew more slowly, were formed, and these did not produce sporangia. On the strong hyphae there were often 2 or 3 sets of sporangia, but always after a time the development of sporangia ceased and the outer portions of the medium became filled with many slender hyphae. One other form which never produced oogonia behaved in a similar manner. The agar here contained an abundance of food, and yet immediately after growth commenced sporangia were formed; while later, when the amount of food present might be thought to have been decreased, no sporangia were formed. At that time no definite experiments were undertaken to explain this phenomenon. Later these cultures were lost, and it was not until the fall of 1913 that another form showing this characteristic was collected. Meanwhile, *A. prolifera*, *A. race-*

mosa, and a number of species of *Saprolegnia* had been cultivated, but none of these produced sporangia in 1.5 per cent agar with pea broth. In the fall of 1913 nos. 67, 68, and 70 were isolated, and in every case the germ tube gave rise to several vigorous hyphae which produced sporangia after attaining a length of some 5 mm.

It was also found that sporangia were sometimes developed on mycelia growing in liquid pea broth. Since there certainly was no question here of an abundant supply of food, the thought suggested itself that KLEBS's conclusion, that sporangium formation takes place only when there is a dearth of food, would not apply to all species. However, when mycelia were transferred to purified water, sporangia were normally produced.

The hypothesis suggested to explain the facts was that although there was plenty of food it did not reach the surface of the growing hyphae rapidly enough; these were therefore soon in an environment poor in food and then sporangia were normally and inevitably produced.

In the pea broth the proteid constituents are colloids, and these large molecules diffuse with extreme slowness, so slowly, in fact, that their movement can be considered to be practically nil. The large, vigorous hyphae which require a relatively large amount of food would therefore after a time find themselves surrounded by a film of liquid out of which they had absorbed the food particles and to which diffusion did not carry new particles as rapidly as the hyphae used them. This condition would result in starvation and the development of sporangia.

To test this hypothesis several series of experiments were prepared as follows. Four Ehrlenmeyer flasks, each holding 100 cc., were half filled with pea broth, sterilized, and inoculated with *A. Klebsiana*. One of these was so hung by a stout string that an arm clamped to a shaft and protected by a cotton pad pushed the flask aside about once a minute. As the flask was pushed aside, it fell against the cotton pad on the end of the arm and thus the liquid was vigorously jarred. Another flask was placed upon a shelf subject to a slight jar from a small motor, so that the surface of the liquid could be seen to tremble slightly; the other flasks were placed upon the writer's desk.

In every case where these flasks were arranged in the afternoon and examined in the morning so that those on the desk would be unaffected by the jar caused by walking, which complicated matters during the daytime, it was found that sporangia had been formed in the flasks on the desk, that the mycelium in the flask subject to frequent shaking showed no sign of sporangia, but consisted of balls of hyphae, the whole very dense and vigorous, and that on the mycelium in the flasks subject to a slight jar there were many aborted sporangia (fig. 1). It was evident that in the latter case a condition of starvation had momentarily existed, stimulating the ends of the hyphae to the production of sporangia; that before these could fully develop, the slight jar of the liquid had resulted in a fresh supply of food being brought to the hyphae, resulting in renewed vegetative growth and the abortion of the partially formed sporangia. The formation of sporangia in the pea agar is doubtless to be accounted for by the slow diffusion of food in the thick medium. The fact that only some species behave in this way doubtless indicates a more vigorous metabolism on the part of such species; the rate of metabolism exceeds the rate of diffusion and the result is starvation.

Saprolegnia Kaufmanniana has also proved interesting in that it shows great sensitiveness to the concentration of haemoglobin in solutions into which vigorous mycelia are placed. While such forms as *S. ferax*, *S. mixta*, or *S. monoica* will produce oogonia more or less freely in concentrations of haemoglobin varying from 0.075 to 0.01 per cent, *S. Kaufmanniana* persistently refused to respond to any concentration except 0.025 per cent. In this, either alone or with certain salts, oogonia containing oospores and accompanied by antheridia were regularly produced, though never in large numbers.

Achlya Klebsiana, n. sp.

This species was collected under three numbers, the plants all proving similar, and all were isolated as single spore cultures during November and December 1913. The cultures were secured from collections of algae from Bass Lake, near Ann Arbor, Michigan, and from near Coldwater, Michigan, in both cases collected by Mr. E. B. MAINS. One culture was also secured from a dish of algae in

the botanical laboratories of the University of Michigan, of unknown source, but doubtless from around Ann Arbor.

Hyphae stiff, medium thick, forming a dense zone about the fly. Among these are large, coarse, branched hyphae attaining a length of 10–15 mm. or sometimes more; sporangia cylindrical, discharging and forming secondary sporangia as in *A. prolifera*, but developing in pea agar or in pea extract when this is absolutely quiet; oogonia on short lateral branches which are about as long as the diameter of the oogonia, rarely at the ends of long hyphae, but nearly always on the basal portions of strong hyphae, near the body of the fly, never intercalary; round or slightly oval in shape; oogonium wall smooth, not pitted, oospores 4–10, averaging about 25 μ in diameter, excentric; antheridia always present, of diclinous origin, partly clasping the oogonia, never clavate nor wrapped about the oogonia; gemmae produced in chains by the breaking up of the large hyphae, cylindrical, sometimes slightly branched or with one or more protuberances at one or both ends.

This species is peculiar in the fact that besides the zone of delicate hyphae which usually surrounds the fly, there were also a number of very long, thick hyphae. These commonly extended for several millimeters beyond the thick tuft of hyphae and spread out on the surface of the liquid, later becoming densely filled with protoplasm and breaking up into chains of gemmae as shown in fig. 2.

Oogonia are produced quite regularly on flies and are always clustered near the body of the fly, but so far, with one exception, I have been unable to secure oogonia in artificial media. In one test a sterilized pea on which the fungus was growing was left in an open dish of distilled water. Bacterial decay set in slowly, the water was changed from time to time, and the fungus kept on growing vigorously, eventually forming oogonia. In no solution of haemoglobin or leucin, with or without salts or sugars, have oogonia with oospores appeared, though empty oogonia have been occasionally formed in haemoglobin. In one case penetration of the oogonium was observed (fig. 3), but whether fertilization takes place is not known. This species shows affinities with *A. DeBaryana* Humphrey in the excentric oospores and smooth unpitted oogonia, but the

strictly diclinous, branched antheridia and the arrangement of the oogonia distinguish it markedly from that species. In *A. DeBaryana* the oogonia are arranged in a loose raceme along the hyphae well out from the fly, while in *A. Klebsiana* the oogonia are always borne in a dense cluster near the body of the fly.

Saprolegnia Kaufmanniana, n. sp.

This species was collected from algal material in the botanical laboratory of the University of Michigan, of unknown source, but presumably from around Ann Arbor.

Vegetative growth like that of *S. ferax,* with firm stiff hyphae; sporangia freely produced and of the same size and appearance as in *S. ferax;* gemmae round, oval, or irregular in shape, mostly single, sometimes in chains and freely produced; oogonia very large, on long or short stalks, or intercalary, scattered; oval or club-shaped, very rarely almost round, the usual size being about 70–80 $\mu \times$ 100–250 μ. The smallest oogonium noted was 30$\times$70 μ; oogonium wall thin and smooth, without pits; oospores from 3 or 4 in small oogonia to very many in large ones, averaging about 20–30 oospores per oogonium; oospores average about 30 μ in diameter, contents granular without any conspicuous oil drop; antheridia nearly always present, only occasionally absent on intercalary oogonia, diclinous, of various shapes from clavate to clasping or irregular, often curving part way round the oogonium, and borne on slender antheridial branches; usually more than one on an oogonium.

This species seems to differ decidedly from all others described, especially in the large, thin-walled oogonia without pits. Rarely two oogonia were observed in series, as in fig. 5. This species may be related to *S. anisospora,* of which species little is known, though no evidence of two kinds of zoospores was found in the present species. Besides its marked morphological characters, *S. Kaufmanniana* is interesting from the fact that it is especially sensitive to the concentration of haemoglobin. Oogonia were but sparingly produced on flies, many cultures having none, and no culture having more than a few. Tests were made by transferring vigorous mycelium to haemoglobin solution, and it was found that only where

the haemoglobin had a concentration of 0.025 per cent were oogonia formed. Of the drawings, fig. 7 is from fly cultures, the others from haemoglobin 0.025 per cent.

S. MONOICA var. **vexans,** n. var.

This was secured from algal material collected at Sukey Lake, near Ann Arbor, Michigan. The vegetative growth, sporangial characters, and the formation and shape of gemmae do not differ in any particular from those present in *S. monoica*, *S. ferax*, or any other species of that group except *S. mixta*, which has weaker hyphae. The material was cultivated for nearly a year and a half on flies, in agar, and by transfer from a strong culture medium such as pea decoction or peptone, into haemoglobin, leucin, peptone, or other solution. During all this time no oogonia were produced. Toward the end of this time a series of tests was being made with several cultures by transferring vigorous mycelium to leucin to which various sugars and salts had been added. Among other combinations there was used leucin $\frac{M}{200}$ + levulose $\frac{M}{200}$, and in this a mycelium out of pea extract produced an abundance of oogonia. When these were examined they proved to be indistinguishable from the oogonia and antheridia of *S. monoica* Prings. Rarely an oogonium was found on which there was no antheridium, but in some solutions this may also be the case with *S. monoica*.

The fact that cultures of *S. monoica* were going on at the same time suggested the possibility of contamination. Check cultures were made, therefore, by taking mycelium from the dish in which the oogonia were formed and growing this on fly. Had the mycelium producing oogonia been that of *S. monoica* (no. 79*c* of my series), plenty of oogonia would have been produced. In fact, no oogonia were formed on the fly culture, but a fresh culture from this fly through pea decoction into leucin and levulose again produced oogonia as before.

We seem to have here, therefore, the remarkable case of a variety of *S. monoica* having lost sexuality, but recovering it under stimulus of this special combination, leucin and levulose in concentration $\frac{M}{200}$ each.

The gemmae of this form are perhaps a little more varied in shape than is the case with the species, but the shape of these organs is so variable in most species that they are of no value for systematic purposes.

Had time permitted, it would have been interesting to cultivate this form for many generations in leucin-levulose solutions to determine whether the vigorous production of oogonia which characterizes such forms of *S. monoica* as my 79*c* would be regained by this variety.

The forms described in this paper are remarkable examples of the intimate dependence of the members of this group on external conditions.

UNIVERSITY OF MICHIGAN

EXPLANATION OF PLATE XXI

FIGS. 1–4.—*Achlya Klebsiana*.

FIG. 1.—Portions of hyphae showing aborted sporangia; tip of one (at *a*) has also died and would shortly have been pushed aside; about ×85.

FIG. 2.—Short chain of gemmae showing how they break away and fall off; about ×85.

FIG. 3.—Oogonium with oospores; ×300.

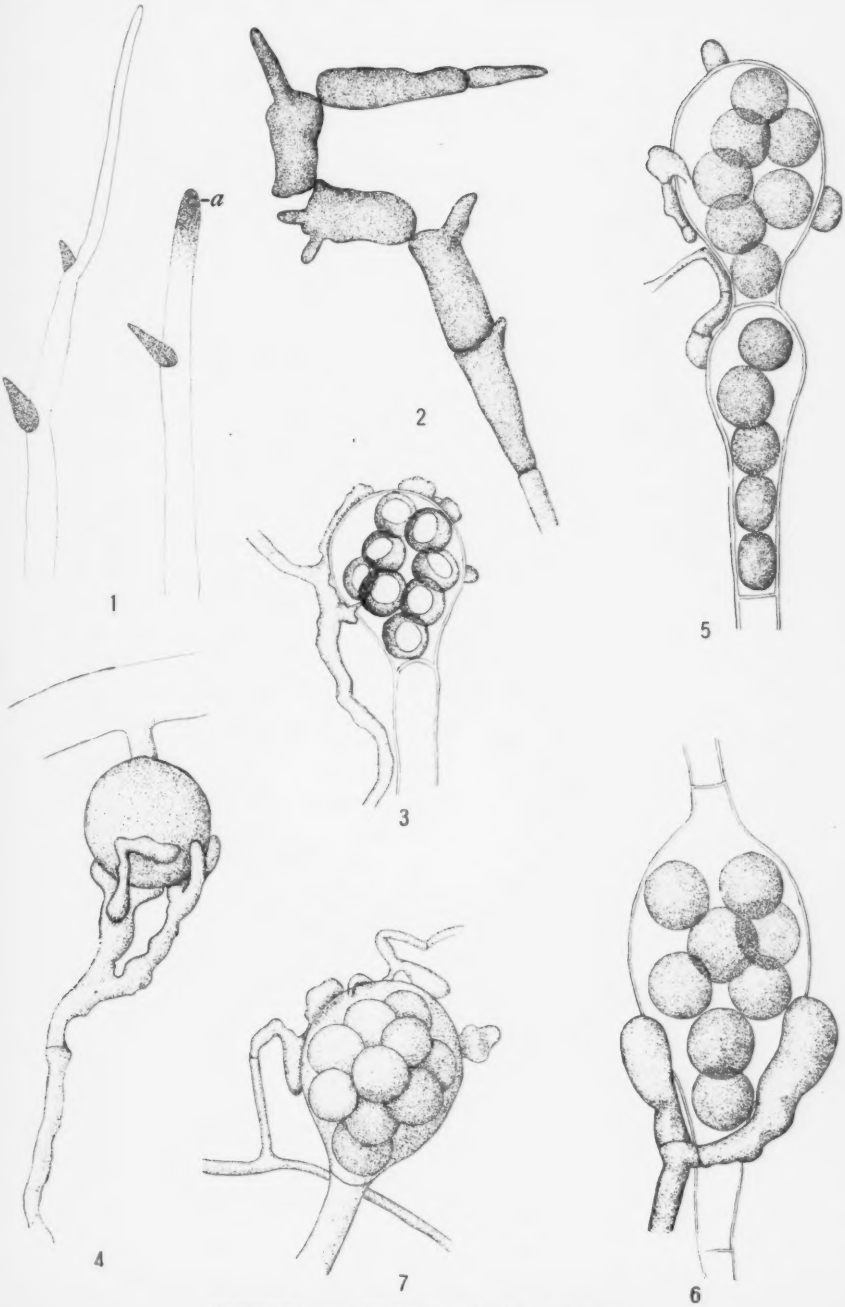
FIG. 4.—Young oogonium showing much branched antheridial hyphae; ×300.

FIGS. 5–7.—*Saprolegnia Kaufmanniana*.

FIG. 5.—Two oogonia in series; ×300.

FIG. 6.—Intercalary oogonium; ×300.

FIG. 7.—Oogonium showing several antheridia; ×300.



PIETERS on ACHLYA and SAPROLEGNIA

BRIEFER ARTICLES

DWARFING EFFECT OF TREES UPON NEIGHBORING PLANTS

The unfavorable effect of trees upon the growth of most plants rooted in the soil immediately about them is generally attributed to one or all of the following influences: (1) undue shade; (2) withdrawal of moisture from soil by the tree roots; (3) withdrawal of nutrient salts by the tree roots; (4) possible excretion of injurious substances into the soil by the tree roots.

Every observing farmer is well aware of the injury to most crops caused by the proximity of tree belts, hedges, or even of single large trees, and the loss caused in this way by trees is often considerable. Undoubtedly partial exclusion of light is an important factor. Cases in which fruit fails to mature may often depend upon this. The writer has found that the black raspberry (*Rubus occidentalis*) grew and flowered freely but failed to ripen fruit in a situation in which the bushes during the earlier half of the day received only one-twelfth to one-fifteenth of the total sunlight, although they were hardly at all shaded during the afternoon.

The present very rainy summer (1915) has afforded a suggestion as to the importance of the second of the factors previously mentioned, the withdrawal of moisture, in dwarfing plants growing under trees. The average rainfall in Boston for July is about 3.24 inches. This year the amount for July was in Boston 8.85 inches and in Cambridge 10.34 inches. The Boston record much exceeds that of any July precipitation during the 44 years for which the Weather Bureau has published a climatological summary of its observations.[1]

During the month of July of the present year the writer noticed that several species of perennial mesophytes which grew just north of and shaded by a belt of deciduous trees (wild cherries, ashes, and maples) were reaching unusual dimensions. Three most notable instances were

[1] No doubt the Cambridge rainfall for July of the present year is also the maximum for a long period. There is no readily accessible summary of total rainfall in Cambridge, month by month.

Aster novae-angliae, *Asclepias tuberosa*, and *Helianthus grosse-serratus*. None of these species was flourishing as well as did other individuals growing in open ground, but all were perhaps twice as tall as during an ordinary season and much more robust than usual. A plant of the moisture-loving *Chelone glabra*, which had for some years barely kept alive, grew luxuriantly and flowered freely.

On the other hand, the rather xerophytic *Sedum telephioides* and *Hedera Helix* showed no better growth than usual, and some other plants, such as *Saponaria officinalis* and *Oxalis corniculata*, showed little increase over their usual size. It would seem that the invariable dwarfing in ordinary seasons of the *Aster*, *Asclepias*, and *Helianthus* previously mentioned must be due mainly to abstraction of moisture from the soil by the roots of the trees. Doubtless many plants of agricultural importance are as sensitive to the effect of diminished water supply as are these three species.—J. Y. BERGEN, *Cambridge, Mass.*

STAMINATE FLOWERS IN ANEMONE

Anemone caroliniana is one of the most common of spring flowers in the vicinity of Grand Island, Nebraska. For several years I have noticed that in a large number of the flowers the pistils are lacking. In 1914 in one collection of 250 specimens, 190 were perfect, 50 had stamens only, and 10 had few or abortive pistils. There were none that had pistils only. The condition found is indicated in table I.

TABLE I

	Stamens			Pistils		
	Minimum	Maximum	Average	Minimum	Maximum	Average
190 normal flowers	20	45	28	25	60	35
50 staminate flowers	7	55	28	.....	.....	.....
10 with few pistils	10	52	40	10	20	16

In 1915 a collection of 133 specimens contained 55 staminate and 78 perfect flowers. A bouquet of especially fine large anemones was also examined. It contained 48 specimens, 46 of which were perfect, and in only 2 of which pistils were lacking. The average number of stamens

in these was 86, the minimum and maximum being 72 and 100. The average number of pistils was 116, the minimum and maximum being 108 and 125. The fact that in these larger and more luxuriant plants the flowers were nearly all perfect and had a large number of both stamens and pistils would suggest that the absence of pistils is due to their degeneration through disease or some other cause; and the case of the 10 flowers with few pistils and an average of 40 stamens would suggest that pistils may be replaced by stamens. There was nothing in the vegetative parts of any of these plants to indicate disease.—CLARENCE J. ELMORE, *Grand Island College, Neb.*

CURRENT LITERATURE

BOOK REVIEWS

Cretaceous plants

The second part of the British Museum *Catalogue of Cretaceous plants*, by STOPES,[1] treats of the flora of the so-called Lower Greensand, which is known on the Continent as the Aptian stage of the Lower Cretaceous. The beds of this age which have escaped erosion and are available for study are nearly all typically marine deposits, with only such traces of terrestrial vegetation as withstood the maceration and trituration of the sea. Consequently, the flora of the Lower Greensand has hitherto been supposed to have been essentially the same as that of the older and better known Wealden deposits. Thus, with the exception of the classic *Bennettites Gibsonianus* of CARRUTHERS and a few cones, the plant remains consist almost entirely of pieces of petrified wood. By a careful study of the latter, STOPES is enabled to list 45 plant forms, comprising 1 thallophyte, 2 Filicales (*Weichselia* and *Tempskya*), 9 cycadophytes, 27 conifers, and 5 angiosperms. Notable features are the presence of angiosperms, the preponderance of conifers, and the scarcity of ferns. Angiosperms have been sparingly represented by leaf impressions in deposits of this age or slightly older, but these have been few in number and vague in character, while these forms of the Lower Greensand, although vague in their affinities, are well characterized.

The proportions of the different groups represented, upon which STOPES lays considerable stress in emphasizing the differences between this flora and other floras of the Lower Cretaceous, is due almost entirely, I believe, to the methods of preservation; that is to say, to differences in the physical conditions of deposition of the sediments. Coniferous remains usually predominate and ferns are scarcely represented in coarse marine deposits. Thus, in the Trinity beds of Texas, which are about the same age as the Lower Greensand, there is but one fern, while there are 8 cycadophytes and 11 conifers. On the other hand, in the Lakota beds of the Black Hills, which are continental deposits partially synchronous with the marine Trinity, there are 13 ferns and only 8 conifers.

The two features of the present work which are of greatest botanical interest are the interpretation of the coniferous woods and the careful description of the wood structure of five indubitable angiosperms of a relatively high degree

[1] STOPES, MARIE C., Catalogue of the mesozoic plants in the British Museum. The cretaceous flora. Part II. London. 1915.

of organization. While they are the oldest angiosperms whose anatomical features are known, they are in no way primitive or pro-angiospermic. The forms, of which three received preliminary treatment in 1912,[2] are named *Cantia arborescens*, *Woburnia porosa*, *Sabulia Scottii*, *Hythia Elgari*, and *Aptiana radiata*. No attempt is made to indicate their family relationships, largely because of our sadly inadequate knowledge of the anatomy of existing dicotyledons. The Coniferae enumerated include, in addition to various forms of *Pinostrobus*, *Cedrostrobus*, and *Abietites*, anatomical material representing a *Sequoia* (Taxodieae), *Protopiceoxylon* (1 sp.), *Pityoxylon* (3 spp.), and *Cedroxylon* (2 spp.) in the Abietineae; four species of *Cupressinoxylon* in the Cupressineae; *Taxoxylon* (1 sp.) and *Podocarpoxylon* (4 spp.) in the Taxaceae. No remains of Araucariaceae are recognized. This list of conifers is of especial interest to American botanists in connection with JEFFREY'S rather sweeping conclusions from his studies of material from the Upper Cretaceous, from which STOPES dissents, apparently on the basis of rather satisfactory evidence.

The present contribution also shows that BUCKLAND'S genus *Cycadeoidea* offers anatomical differences from the American forms usually described under that name. A new cycadophyte trunk is made the type of a new genus, *Colymbetes*. It is found in the lower part of the Lower Greensand and may have been derived mechanically from the underlying Wealden sediments. The climate of the Aptian is considered to have been less warm than that of the preceding Wealden.

The book on the whole is an exceedingly valuable contribution to our knowledge of fossil plants, particularly to that important part of the Lower Cretaceous represented in Britain by the Lower Greensand.—EDWARD W. BERRY.

Flora of New Zealand

Two quarto volumes illustrating the New Zealand flora have appeared under the editorship of T. F. CHEESEMAN, curator of the Auckland Museum, with the assistance of W. B. HEMSLEY.[3] The 250 plates are exceptionally good, having been drawn by Miss MATILDA SMITH of the Kew Herbarium, whose work in connection with the *Botanical Magazine* and *Icones Plantarum* has long been known. Accompanying each plate there is an account of the discovery and occurrence of the plant, as well as items of general interest. Since the technical descriptions are published in the *Manual of the New Zealand flora* (1906) they are not repeated in the *Illustrations*.

The problem of selecting approximately 265 plants to illustrate adequately such a flora as that of New Zealand can be appreciated. The main features of the flora, however, have been presented, and no important genus or group

[2] STOPES, M. C., Phil. Trans. Roy. Soc. London. B **203**:75–100. *pls. 6–8*. 1912.

[3] CHEESEMAN, T. F., Illustrations of the New Zealand flora. 2 vols. 4to. *pls. 250*. Published under the authority of the government of New Zealand. Wellington. 1914.

is without proper representation. The alpine flora has received full treatment, and special attention has been paid to the endemic genera. The editor says that he has also illustrated a number of plants of special interest "either on account of their economic value, or from biological or morphological reasons, or from their peculiar geographical distribution." He has not thought it necessary, however, except in a few special cases, to figure plants occurring in other countries as well as New Zealand.

It is interesting to note the result of the selection, as expressing in a general way the editor's opinion of what constitutes the main features of the New Zealand flora. Without going into detail, it may be stated that the families represented in this selection by more than ten species are as follows: Compositae (35), Gramineae (17), Filices (17), Orchidaceae (15), Umbelliferae (12), Scrophulariaceae (12).—J. M. C.

MINOR NOTICES

Pharmacognosy.—KRAEMER[4] has published a textbook of pharmacognosy which is encyclopedic in its wealth of information. He recognizes the synthetic character of the subject, especially in its combination of botanical and chemical aspects. Moreover, both of these aspects are shown to involve the ecological conditions under which plants grow, so that scientific pharmacognosy is a very complex subject. After an introduction dealing with the problems involved, the great plant groups are presented, the large majority naturally being families of angiosperms, 94 in number, from which drugs are obtained. As stated by the author, the book is intended for students of pharmacy, pharmacists, food and drug analysts, and pharmacologists. We might add to this list students of economic botany, for pharmocognosy is one of the great fields of applied science.—J. M. C.

Citrus fruits.—COIT[5] has published as a volume of BAILEY'S "Rural Science Series" an account of the citrus fruit industry, with special reference to the requirements and practices for California. It seems that the citrus industry has not only reached a high state of development in California and Florida, but is still progressing rapidly. The present volume discusses the underlying principles in such a way as to emphasize the importance of certain fundamentals which must be kept in mind. The industry as it exists at present is described, and all current information that seems valuable is organized and made available. Of special interest to the botanist are the chapters dealing with the geography and climate of California, the gross structure and habits of growth of citrus plants, and the citrus diseases and their control.—J. M. C.

[4] KRAEMER, HENRY, Scientific and applied pharmacognosy. 8vo. pp. viii+857. *figs. 313*. Published by the author, 145 North 10th St., Philadelphia. 1915.

[5] COIT, J. E., Citrus fruits. 8vo. xx+520. *figs. 151*. New York: Macmillan. 1915.

Ferns of South Africa.—SIM[6] has prepared a second edition of his *Ferns of South Africa*, bringing together in this convenient form much widely scattered information. The preliminary chapters deal with the following topics: ferns, parts of ferns, reproduction and propagation, cultivation, identification and preservation, the ferns of South Africa, the natural home of ferns. The bulk of the volume naturally is concerned with the descriptions of species. Attention is called to the fact that the number of species of ferns in South Africa is remarkably small compared with the whole flora. The present volume contains 220 species of ferns and fern allies, an increase of 41 species over the first edition, published in 1892. The full descriptions and the numerous plates make the volume very complete for its purpose.—J. M. C.

Western wild flowers.—MARGARET ARMSTRONG,[7] in collaboration with Professor J. J. THORNBER of Arizona, has prepared a popular field book describing and illustrating the "common wild flowers" west of the Rocky Mountains. The book is "popular," not merely in the selection of plants for description, but also in the absence of technical terminology. The author says that "almost all technical botanical terms have been translated into ordinary English." The drawings for the numerous illustrations have all been made from life, and, in connection with the "ordinary English" of the text, should enable the "general public" to identify the conspicuous plants in which it may have a casual interest.—J. M. C.

Plant life.—This title has been selected by HALL[8] for a volume presenting the plant kingdom "to the amateur botanist and the lover of nature." As a consequence, the style is not technical, but appeals to general interest. The illustrations are numerous, and 50 of the 74 plates are colored. Some idea of the topics presented can be obtained from the chapter heads, which are in effect as follows: asexual plants, development of sex in plants and a study in evolution, seaweeds, fungi and lichens, archegoniates, phanerogamia, fossil plants, food of plants, perpetuation of the race, defenses of plants, ecology.—J. M. C.

NOTES FOR STUDENTS

Origin of monocotyledony.—In an address delivered at the twenty-fifth anniversary celebration of the Missouri Botanical Garden, COULTER,[9] because of continued studies on the origin of monocotyledony, chiefly in grasses,

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[6] SIM, THOMAS R., The ferns of South Africa. 2d ed. 8vo. pp. ix+384. *pls.* 186. Cambridge University Press. 1915. *25s.*

[7] ARMSTRONG, MARGARET, Field book of western wild flowers. 16mo. pp. xx+596. *col. pls. 48. figs. 500.* New York and London: Putnam, 1915. $2.00.

[8] HALL, CHARLES A., Plant life. 8vo. pp. xi+380. *pls. 74. figs. 80.* London: A. & C. Black. 1915.

[9] COULTER, J. M., The origin of monocotyledony. Ann. Mo. Bot. Gard. 2:175–183. *figs. 9.* 1915.

restated the conclusions previously arrived at from a study[10] of *Agapanthus umbellatus* and some other monocotyls as follows: "In the embryogeny of both monocotyledons and dicotyledons, a peripheral cotyledonary zone gives rise to two or more growing points, or primordia; this is followed by zonal development, resulting in a cotyledonary ring or sheath of varying length. If both growing points continue to develop equally, the dicotyledonous condition is attained; if one of the growing points ceases to develop, the continued growth of the whole cotyledonary zone is associated with that of the other growing point, and the monocotyledonous condition is attained. In like manner, polycotyledony is simply the appearance and continued development of more than two growing points on the cotyledonary ring. It follows that cotyledons are always lateral structures, arising from the peripheral zone developed at the top of a more or less massive proembryo. This reduces cotyledony in general to a common basis in origin, the number of cotyledons being a secondary feature. The constancy in the number of cotyledons in a great group is no more to be wondered at than the same constancy in the number of petals developed by the petaliferous zone."

To those whose mental processes require a "type" for everything, the embryogeny of the grasses is very puzzling, because it does not conform to the hitherto accepted monocotyl "type" of embryogeny. The structures have received the names "scutellum," "epiblast," and "coleoptile." Early in the history of the subject the scutellum was recognized as the cotyledon. The epiblast was recognized as a second and rudimentary cotyledon from its first discovery until the time of SCHLEIDEN, who in 1837 so clamorously dissented from this view that it was suppressed from the literature of the subject until 1897, when VAN TIEGHEM, studying the embryogeny of grasses, reaffirmed that the epiblast is a second cotyledon. In the meantime HANSTEIN, followed by FAMINTZIN, had made a study of *Alisma*, which has a filamentous and therefore highly specialized proembryo, and fixed what has been almost universally regarded as the monocotyl "type" of embryo. Because of these first studies, the massive proembryo, so prevalent in monocotyledons, has been called the "aberrant type," although it is undoubtedly the more primitive and generalized, while the filamentous proembryo is the more specialized. About two-thirds of the grasses show a well marked second cotyledon. This second cotyledon is quite pronounced in those grasses which have a relatively long internode ("mesocotyl" of English anatomists) between the cotyledons and the "coleoptile" or bud-scale leaves.

COULTER shows that there is a progressive reduction of the second cotyledon until *Zea Mays* is reached, where the only external sign of the second cotyledon is a small hump opposite the functional cotyledon; but even here a small procambium is present, being exactly opposite the procambium of the

[10] COULTER, JOHN M., and LAND, W. J. G., The origin of monocotyledony. BOT. GAZ. **57**:509–519. *pls. 28, 29.* 1914.

functional cotyledon. The absence of a vascular strand in the smaller cotyledon has been used as evidence to prove that it is not a second cotyledon. The reviewer has no doubt that when a relatively great quantity of material shall have been studied a procambium will occasionally be found in the second cotyledon. It is unfortunately the habit of some investigators to make sweeping conclusions from an examination of a very small quantity of material.

The facts shown by this reinvestigation of the grasses are as follows: "The terminal cell of the proembryo forms a group of cells; the peripheral cells of the group develop the cotyledonary ring or sheath, on which two growing points appear. One of these growing points soon ceases to be active, and the whole zone develops in connection with the other growing point; but at the base of the growing cotyledon a notch is left by the checking of the growing point. This notch is really the space between the two very unequal cotyledons which surround the real apex of the embryo. The apex of the embryo is at the bottom of the notch, and not at the tip of the large embryo. This apex soon begins to form leaves, and the so-called stem tip appears issuing from the bottom of the notch, in a relation apparently lateral only because the two cotyledons are so unequal. Furthermore, when the stem tip is examined, it is found not to be a stem tip, but a cluster of leaves, whose rapid development has aborted one of the growing points on the cotyledonary zone. All this is very obvious in grasses and is equally obvious in any massive proembryo, but it escaped the earlier observers of filamentous proembryos."

The general conclusion is that "monocotyledony is simply one expression of a process common to all cotyledony, gradually derived from dicotyledony, and involving no abrupt transfer of a lateral structure to a terminal origin."—W. J. G. LAND.

Anatomy of Helminthostachys.—In the third of his series of papers on the Ophioglossaceae, LANG[11] gives the results of a reinvestigation of the anatomy of the rhizome of *Helminthostachys*, together with the details of the vascular connections of two branching specimens. In rhizomes of young plants, the xylem forms a solid strand of two kinds of tracheids; those of the outer part having pitted walls, while the inner elements are smaller and are spirally thickened. By comparison with the bases of branch steles, where a similar condition exists, and by examination of the origin of leaf traces, where the protoxylem becomes evident, it is shown that the two kinds of elements in the juvenile type of stele are outer and inner metaxylem, respectively; and that therefore the stele of *Helminthostachys* is mesarch even in the juvenile condition. The transition to the adult condition begins by the appearance of parenchyma cells among the tracheids of the inner metaxylem, thus forming a mixed pith. In the adult condition the stele is greatly expanded and the pith is large.

[11] LANG, WILLIAM H., Studies in the morphology and anatomy of the Ophioglossaceae. III. On the anatomy and branching of the rhizome of *Helminthostachys zeylanica*. Ann. Botany **29**:1–54. *pls. 1–3. figs. 7.* 1915.

All stages between the juvenile type with the solid stele and the adult type may occur; cases of reduction of steles of the adult type to the juvenile condition are described. These variations are held to be dependent upon physiological factors; the solid stele of the juvenile type is considered to be merely a physiological variation of the general type of the species.

The outer xylem of the leaf trace, after separation from the stele, curves round the protoxylem strand; at the same time, the trace, originally monarch, becomes diarch by the division of the protoxylem strand. These two processes result in the formation of a trace whose cross-section shows two protoxylem points, each surrounded by metaxylem. This "clepsydroid" stage of the leaf trace is characteristic of certain of the Zygopterideae and affords data for a comparison with that group.

The branches develop from the vestigial axillary buds. There is no vascular connection between the branch stele and the leaf trace immediately below, as in some species of *Botrychium*. Immediately below the point of origin of a branch, accessory xylem is developed by irregular divisions of the parenchyma within the phloem. While no cambium is present, this is considered to be a form of secondary thickening. In the base of the branch this accessory xylem surrounds an extension of the inner metaxylem of the main axis, thus forming a solid xylem strand which is in all respects similar to the steles of rhizomes of young plants. The further development of the branch stele is identical with that of steles of young plants.

The mesarch character of the stele, the clepsydroid stage of the leaf trace, the irregular secondary thickening of the stele, and the connection of the branch stele with the main axis rather than with the leaf trace, all emphasize the view of relationship of the Ophioglossaceae to the Zygopterideae. It is further pointed out that these features also afford a basis for comparison with certain of the Cycadofilicales.—L. C. PETRY.

Origin of dwarf plants.—STOUT[12] has described a dwarf form of *Hibiscus oculiroseus* which differs from the usual robust type in having more basal branches, shorter internodes, and smaller, somewhat crinkled and irregular leaves. The dwarfs are descendants of a single robust plant with some crinkled leaves and somewhat shortened upper internodes, a type known as "intermediate." Four other plants have given none but normal robust offspring, something over 100 in all. Selfed seed from the intermediate plant produced 45 plants, all dwarf. Open-pollinated seed from the same plant yielded one dwarf, 3 intermediates, and 11 robust plants. From selfed seed of one robust plant, there were grown one intermediate and 33 robust plants. Selfed seed of the one dwarf plant produced one robust, 8 intermediate, and 72 dwarf plants, the robust plant being apparently an accidental hybrid. These results are compared with the behavior of dwarfs of *Oenothera*, peas, and sweet

[12] STOUT, A. B., The origin of dwarf plants as shown in a sport of *Hibiscus oculiroseus*. Bull. Torr. Bot. Club 42:429–450. 1915.

peas. The author emphasizes the fact that in the dwarf *Hibiscus*, as well as in dwarfs of other plants, numerous characters besides stature are modified, and expresses doubt concerning the possibility of interpreting such phenomena as due to a change in a single hereditary unit. The reviewer is inclined to suggest that, until there are available adequate data derived from crosses between the new and the normal types, little is to be gained by the assumption of either single or plural genetic changes, or indeed by a discussion of any other hypothesis.—R. A. EMERSON.

Growth of sugar cane.—KUYPER[13] has investigated the growth of the leaf blade, leaf sheath, and stalk of sugar cane. His method was to make some holes (with a darning needle) through the young leaves and internodes. The distance between holes was made as uniform as possible; in practice the spacing could not be much less than a centimeter. After several days the leaves were removed, one after the other, and the distance between the holes measured. By comparing these measurements, the rate of growth of an area on different parts of the leaf, and on different leaves, can be determined. The results indicated that the region of most rapid growth moves basipetally over the blade, then over the sheath, and finally over the internode. The region near the base continues its growth after the regions above have completed their development. These conclusions were confirmed by measurements obtained from equally spaced lines of India ink, and also by cell measurements. Regarding an internode bearing a leaf at its summit as the unit of structure, it may be said that the blade first becomes fully grown, then the sheath follows, and finally the internode develops. KUYPER shows how these conclusions may be applied in studying the "top rot" disease of Java. The cause of the disease must be sought in temporary unfavorable conditions of growth, and this investigation furnishes a method of recognizing the period of growth influenced by these conditions.—J. M. C.

Stomata of sugar cane.—KUYPER[14] in connection with an investigation of the transpiration of sugar cane discovered a lack of knowledge of the structure of the stomata. Several methods were tried for measuring the width of the stomatal cleft. Direct measurements with the microscope proved impossible, not only because it is very difficult to make good preparations of the leaf for this purpose, but also because the variations in the opening are very small. Since, however, the application of the infiltration method of Miss E. STEIN showed that great variations really exist in the rapidity with which paraffin and kerosene penetrate the leaf tissue, it was clear that there must be something in the structure of the stoma which could explain this variation. The

[13] KUYPER, J., De groei van bladschyf, bladscheede, en stengel van het suikerriet. Archief voor de Suikerindustrie in Nederlandsch Indië **23**:528–540. *pls. 2.* 1915.

[14] KUYPER, J., De bouw der huifmondjes van het suikerriet. Archief voor de Suikerindustrie in Nederlandsch Indië **22**:1679–1707. *figs. 6.* 1914.

figures of transverse sections of stomata show that any noticeable widening of the slit in the ordinary way is impossible, because of the very thick cell walls. The guard cell, however, can move a little as a whole, because it is distinctly hinged with the adjacent cell. The general conclusions reached are as follows: a movement as described by SCHWENDENER for grass stomata is impossible; the guard cells can vary their distance from each other to a slight extent by changing their position among the surrounding epidermal cells; the position and structure of the neighboring cells makes it possible to change the length of the slit in the vertical direction.—J. M. C.

Internal temperatures of plants.—PEARSON[15] has made observations on internal temperatures of the stems of *Euphorbia virosa* and *Aloe dichotoma* at 4200 ft. altitude, on the western flanks of the great Karasberg Range in Great Namaqualand. *Euphorbia* reached its maximum at about 2:00 P.M., about the same hour as the shade maximum; while *Aloe* attained its maximum after sundown. In *Euphorbia* the highest internal temperature observed was 51°.5 C.; the greatest range of internal temperature was 27°.5 C.; and the excess of internal over shade temperature 15°.35 C., as against 38°.5, 16° C., and 5° C. respectively for *Aloe*. These observations were made in December. It is likely that in February and March both the internal maximum temperature and the excess over shade temperature is much greater. Xerophytes have much reduced transpiration, the greater of the two cooling methods in mesophytes, and depend largely upon thermal emissivity for cooling. Even in mesophytes as great difference between shade and internal leaf temperatures have been observed as are recorded here, and in xerophytes much greater differences. The author observes that wounding *Euphorbia* causes a considerable fall in the internal temperature. This is due partly to expansion of gases in the air chambers and partly to rapid evaporation from the wound.—WILLIAM CROCKER.

Javanese Pallavicinias.—CAMPBELL and Miss WILLIAMS[16] have recently completed a study of three species of *Pallavicinia* collected by Professor CAMPBELL in Java in 1906. The apical cell in the three species is dolabrate, being similar to the usual condition in *P. Lyellii*, which, however, the reviewer has observed rarely has a triangular pyramidal cell similar to the one in *P. decipiens*. The antheridium in development shows the usual situation among Jungermanniales. A delicate wall separates the pairs of spermatocytes. No "Nebenkörper," reported by IKENO for *Marchantia*, was found. The archegonia present few variations from the usual liverwort conditions. In *P.*

[15] PEARSON, H. H. W., Observations on the internal temperatures of *Euphorbia virosa* and *Aloe dichotoma*. Annals Bolus Herb. 1:41–66. 1914.

[16] CAMPBELL, D. H., and WILLIAMS, FLORENCE, A morphological study of some members of the genus *Pallavicinia*. Leland Stanford Jr. Univ. Pub. 7, Univ. Series, pp. 44. *figs. 23.* 1914.

radiculosa the primary cap cell may also add to the neck of the archegonium, but contributes nothing to the axial row. In this species the neck canal cells range from five to six. The embryo, while not different from that of other Anacrogynae, closely resembles *Aneura* in that a large haustorial, suspensor-like cell is produced. In the capsule the sterile cap is pronounced, and in consequence the dehiscence is by means of four longitudinal slits. The authors conclude that the evidence does not warrant the erection of the two families Aneuraceae and Blyttiaceae.—W. J. G. LAND.

Brown oak.—GROOM[17] has investigated the cause of what is known as "brown oak" or "red oak" in Great Britain. The phenomenon consists in the replacement of the ordinary heart wood of *Quercus Robur* by a firm, richer toned, often reddish brown wood, which varies in tint from dull brown to rusty brown. It is found to be due to the influence of a fungus which lives exclusively in the heart wood, which it infects through wounds. "Brown oak" usually occurs at the base of the trunk and in the adjoining root and extends more or less upward in the stem and downward in the root. If the fungus gains entrance to the upper parts of the tree, it produces in these regions masses of "brown oak." The color is due to the fact that the fungus produces a brown substance in the individual cells which is highly resistant to solvents. The source of the food of the fungus was not determined, although there are reasons to believe that tannin is one of the sources. The identity of the fungus is also left in doubt. It produces conidiophores resembling those of *Penicillium*, and on certain specimens basidiocarps appear, which were identified as a species of *Melanogaster*, but cultures did not establish any connection between the two phases.—J. M. C.

Morphology of Arisaema.—PICKETT[18] has made a careful study of *Arisaema triphyllum*, and has contributed materially to our knowledge of the morphology of the Araceae. The critical situations may be summarized as follows: There is a wide range in time in the development of the flowers, with a strong tendency to the earlier development of staminate flowers. The tapetal nuclei of the microsporangium are freed and "wander" among the developing microspores, as DUGGAR has described for *Symplocarpus*. The embryo sac is of the *Lilium* type, and a complex and permanent suspensor system is developed. The endosperm arises from one of the daughter cells (micropylar) of the primary endosperm nucleus, the other daughter cell not dividing. The primary roots are diarch, while the secondary roots of seedlings and all roots of mature plants are triarch to pentarch. The statement is made that the sex of mature plants is changeable, dependent upon the amount of available water.

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[17] GROOM, PERCY, "Brown oak" and its origin. Ann. Botany **29**:393–407. 1915.

[18] PICKETT, F. L., A contribution to our knowledge of *Arisaema triphyllum*. Mem. Torr. Bot. Club **16**:1–55. *pls. 1–5. figs. 70.* 1915.

Occasionally flowers are also found showing a tendency to become bisporangiate.—J. M. C.

Physiology of parasitism.—BROWN[19] has begun a much needed investigation of the physiological relation of host and parasite, his first paper dealing with *Botrytis cinerea*. From the germ tubes of this fungus he succeeded in obtaining a very powerful extract, whose action on cell walls results in the disintegration of tissue, and whose action on the protoplasts produces death. This extract loses its "lethal power" by heating, by mechanical agitation, and by neutralization with an alkali. Neither oxalic acid nor oxalates are accountable for the toxicity of the extract, which the author concludes must be due to the presence of a substance of colloidal nature. The only active substance discovered was an enzyme which was thought to be responsible for the lethal action of the extract. The multiplication of such investigations will result in some progress in knowledge as to the nature of immunity and susceptibility.—J. M. C.

Morphology of Ephedra helvetica.—In a thesis presented for the doctorate of science at the University of Geneva, SIGRIANSKI[20] has reviewed and reinvestigated *Ephedra helvetica*. Two new facts are reported. The hypodermal archesporial cell does not divide periclinally and give rise to a primary wall cell. By division of the cells of the epidermis the hypodermal initial is placed deeply within the nucellus. The figures which illustrate this situation will not entirely satisfy a critical investigator. A second and most important fact is that the four megaspores are all functional, the wall of the megaspore mother cell being the embryo sac wall, as in *Lilium* and some other angiosperms. It would be most interesting to know with certainty whether *Welwitschia* and *Gnetum* have attained the *Lilium* level in this respect.—W. J. G. LAND.

Jurassic wood.—Miss HOLDEN[21] has described a new species of *Metacedroxylon* from the Jurassic of Scotland, under the name of *M. scoticum*. It is a good illustration of the merging of araucarian and abietinean characters during the Jurassic, since it is araucarian in the pitting of the tracheids, and abietinean in the pitting of the rays. It differs from *M. araucarioides* only in the absence of pits on the tangential walls of the tracheids and in the biseriate character of the rays.—J. M. C.

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[19] BROWN, WILLIAM, Studies in the physiology of parasitism. Ann. Botany **29**: 313–348. 1915.

[20] SIGRIANSKI, ALEXANDRE, Quelques observations sur l'*Ephedra helvetica* Mey. pp. 62. *figs.* 74. Geneva. 1913.

[21] HOLDEN, RUTH, A Jurassic wood from Scotland. New Phytol. **14**: 205–209. *pl.* 3. 1915.

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